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A VEGETATION AND SOIL CHRONOSEQUENCE ON THE MESABI IRON RANGE SPOIL BANKS, MINNESOTA

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INTRODUCTION

In contrast to the rather voluminous literature concerning artificial reforestation of industrial waste land, especially strip-mined areas, comparatively few studies have been made of the development of natural vegetation. This is to be expected, since many states require by law that all of their strip-mined lands be reforested by the companies concerned. Even in localities not affected by this law, artificial reforestation projects have been carried on for many years.

Croxtan (1928) described the natural revegetation of coal strippings in southern Illinois. The overburden which was removed and formed into spoil banks consisted of a mixture of agricultural soil, glacial till, clay, shale, limestone, and poor-grade coal. The last contained considerable quantities of iron pyrite which upon weathering produced sulfuric acid and a resultant pH of 4 or less in the immediate area. In such places vegetation failed to become established. On areas of pH 5 or greater vegetation developed rapidly. *Convolvulus sepium*, *C. arvensis*, *Ipomea hederacea*, and certain grasses, especially *Setaria* sp., appeared within a few days following deposition of the overburden, arising from roots and rhizomes contained within the strippings. These were followed within 2 or 3 yrs by numerous weeds, especially *Polygonum pennsylvanicum*. Within 5 yrs, *Melilotus alba* became dominant on circumneutral areas, but did not invade areas with a pH less than 5. At about this time, woody plants entered the succession, *Populus deltoides* and *Platanus occidentalis* being the most abundant.

Whyte & Sisam (1949) summarized the work which

had been done in England as well as the Illinois study mentioned above. They emphasized that the nature of any natural spoil bank community is determined by (1) the nature of the spoil bank, (2) the nature of the adjacent vegetation, and (3) the habitat requirements of this vegetation. McLean, as reported by Whyte & Sisam, described the succession on South Wales spoil banks leading to a climax woodland of *Betula pubescens* and *Salix aurita*. Hepburn, also cited by Whyte & Sisam, recorded the succession on spoil banks at Corby, Northampton. A more or less continuous grassland was formed after 20 yrs of plant development.

Rogers (1951) briefly described the natural revegetation of spoil banks in Arkansas, Oklahoma, Kansas, Missouri, and Iowa. Herbaceous weeds were common invaders and *Populus deltoides* the most important woody pioneer. The rate of succession and density of cover depended to a large extent on the acidity, texture, and stability of the banks.

Tryon & Markus (1953) made an excellent study of the natural revegetation of West Virginia iron-ore spoil banks. The banks ranged in age from 72 to 131 yrs. Both herbaceous and tree growth data were obtained and compared with similar data from adjacent control areas on undisturbed land and were found to be quite similar. This indicated that these spoil banks could be utilized effectively for timber or forage production.

The climate, native vegetation, and spoil bank material along the Mesabi range differ greatly from any discussed in these prior studies. The study reported in this paper was initiated in the hope that such

differences might yield results which would increase our knowledge of the kind and rate of plant successions and the rate of soil development.

Grateful acknowledgement is made to the following for guidance, assistance, and special courtesies: Dr. D. B. Lawrence, Dr. H. C. Hanson, my wife Marie, M. A. Hanna Co., Jones & Laughlin Steel Corp., Snyder Mining Co., W. S. Moore Co., Pickands Mather & Co., The Cleveland-Cliffs Iron Co., Meridan Iron Co., Minnesota Department of Conservation, and the Soils Department of the University of Minnesota. Financial assistance was provided through the Anderson Summer Fellowship and the Taconite Fellowship from the University of Minnesota and a grant from the Minnesota Institute of Research.

GENERAL DISCUSSION OF THE MESABI RANGE

The Mesabi range, located in northeastern Minnesota, is the largest iron-ore deposit in the United States. Through 1950, the total shipment of this ore from the Mesabi exceeded 1,700 million gross tons accounting for more than two-thirds of the total production of the entire Lake Superior district and more than one-half of the total production of the entire United States (Wade 1951).

"Mesabi range" designates the preglacial outcrop area of the Bivabik formation now mostly buried under glacial till. One-fourth to three miles wide, it extends northeast for 120 mi. from eastern Cass County through Itasca County to the eastern edge of St. Louis County (Fig. 1).

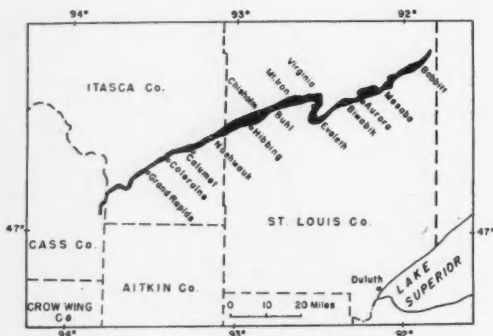


FIG. 1. Map of the Mesabi district (adapted from White 1954).

GEOLOGICAL HISTORY

The Ely greenstones and Laurentian granites, the oldest rocks in the Mesabi range region, were formed during the Archeozoic era and represent metamorphosed lavas and igneous intrusions respectively.

The deposition of great quantities of muds and sands occurred at the beginning of the Proterozoic era, and these, plus volcanic ash and other material, were compacted and cemented to form the Knife Lake slates, more than 5,000 ft thick. Following this came the intrusion of a huge granitic batholith.

At or about this time, the overlying Knife Lake slates were folded and faulted into an extensive range of elevations called the Algonian Mountains. A long period of erosion followed during which much of the Algonian Mountains was eroded away exposing areas of the underlying granites and greenstones. The area was then covered by a sea which deposited the sand and gravel that have since formed the Pokegama quartzite. The iron and silica in solution in this sea were then precipitated and deposited to form the Biwabik iron formation, consisting largely of taconite. While the sea still covered this area, the deposition of huge quantities of clayey muds covered the Biwabik formation to a depth of several thousand feet. These muds were compacted to form the Virginia slates. Following an erosion interval, outpourings of lavas and the intrusion of Duluth gabbro occurred. The resultant heat recrystallized much of the Biwabik iron to magnetic taconite toward the eastern end of the Mesabi range. During this period of volcanism, the Lake Superior basin was depressed, tilting all of the rock formations of northeastern Minnesota toward the southeast.

A period of 500 million years followed, extending through the Paleozoic era and into the Mesozoic era, during which the dominant process was one of erosion. Early in this period, the Biwabik taconites were exposed, and percolating water leached out much of the silica leaving behind concentrations of iron oxides which constitute the high grade ores. During the Mesozoic era, a minor invasion of the Cretaceous Sea occurred depositing fossiliferous sediments and accumulating iron-ore pebbles locally.

During the Cenozoic era, the most significant event was the deposition of Pleistocene glacial drift, covering practically all of northeastern Minnesota's bedrock formations. Discussion of the history of Pleistocene glaciation as it applies to northeastern Minnesota is restricted to the Wisconsin Period, since the earlier Nebraskan, Kansan, and Illinoian drifts have not been found in this area. Of the four major substages of the Wisconsin, only the Cary and Mankato contributed to the present mantle of glacial drift.

Sardeson (1916) and Leverett (1932) described a relatively simple sequence. Two principal drifts were recognized, the Middle-Wisconsin or Cary red drift of the Patrician ice sheet and the overlying Late-Wisconsin or Mankato gray drift of the Keewatin ice sheet. The Patrician ice sheet, centered southwest of Hudson Bay, entered northeastern Minnesota and advanced southward across the Mesabi range.

The Keewatin ice sheet entered northwestern Minnesota during the Mankato substage and advanced southward to form the Des Moines lobe. A segment of the Des Moines lobe, the St. Louis sublobe, advanced eastward across northern Minnesota almost to Lake Superior. Contemporaneous with the advance of the Keewatin ice sheet, the Superior lobe from the Labradorian center moved down the Lake Superior basin and formed a narrow contact zone

with the St. Louis sublobe about 30 mi. west of Duluth.

Recent work, however, has indicated that the Cary and Mankato substages were probably much more complex. Wright (1954), using stratigraphic and lithographic evidence, has proposed 5 and possibly 6 lobes for the Cary substage and modified the Mankato substage in certain respects. Applying this new sequence to the Mesabi range district, the overlying glacial drift was deposited by 3 ice sheets, the Brainerd lobe during the Cary substage and the Superior lobe and St. Louis sublobe during the Mankato substage. The Brainerd lobe from the northeast deposited a brown, sandy till corresponding to the Middle-Wisconsin or red drift of Sardeson and Leverett. The Superior lobe and St. Louis sublobe are still considered to have advanced contemporaneously during the Mankato substage. However, it is believed that the advance of the St. Louis sublobe created an obstruction which caused a bifurcation of the advancing Superior lobe at the contact zone west of Duluth. One of these sublobes turned northward reaching the Mesabi range and depositing a layer of red, clayey till derived from the Lake Superior basin. Upon retreat of the Superior lobe, the St. Louis sublobe made a slight final advance depositing an overlap of gray or buff till on the Superior red till.

Thus the mantle of glacial till which overlays the Biwabik iron formation generally consists of three distinct types: a lower brown, sandy till; a red, clayey till; and an upper gray or buff till. The brown and red tills are somewhat acid in nature, while the gray or buff till with numerous limestone pebbles is slightly alkaline or circumneutral.

MINING OPERATIONS

The first mine on the Mesabi range opened in 1892 and was quickly followed by others all along the range. The rather shallow depth of the overburden, which may vary from practically zero to 350 ft, makes open pit mining (Fig. 2) the most practical and economical kind of operation on the range, although there are a number of successful underground mines also. In open pit mining, the glacial till is stripped from the underlying ore by power shovel or drag line and transported to nearby dumping areas by train, truck, or conveyor belt. These man-made hills and plateaus of glacial till are called stripping dumps or spoil banks.

Much of the lean ore which had been mined, especially taconite, has been stockpiled for future use in lean-ore dumps or spoil banks. With the recent advances in the processing of taconite, these lean-ore spoil banks can be considered at best only transitory. In fact many of the lean ore banks are being reworked and the taconite shipped to processing plants at the present time.

PRIMARY SUCCESSION

A primary succession may be defined simply as any vegetational development initiated on a previously unvegetated substrate. It is now recognized by most

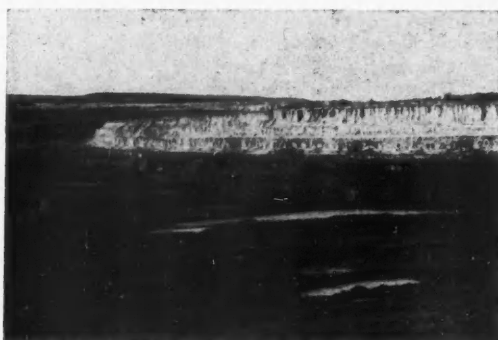


FIG. 2. General view of open pit mine showing lighter colored glacial till overlying darker iron ore.

ecologists that the kind of vegetation which comprises the succession and the rate of development of this succession depends upon a number of factors. Similarly the kind of soil profile developed and its rate of development is dependent on many factors. This concept of a multiplicity of factors governing any ecosystem or portion of that ecosystem was first developed in the science of pedology. Jenny (1941), basing his ideas on many previous studies especially those of Dokuchaev, formalized "the fundamental equation of soil forming factors,"

$$s = f(\text{cl, o, r, p, t})$$

where the soil and its properties are considered a function of environmental climate, organisms, relief, parent material, and time. This equation was utilized by Major (1951) in his proposition that these same 5 factors determined plant communities and the properties of these communities.

$$v = f(\text{cl, o, r, p, t})$$

At the present state of knowledge, such equations are incapable of being solved mathematically, nor is it likely that such actions and interactions of these functions will ever be expressed in truly concrete numerical terms. Yet these theoretical equations have been and will continue to be extremely important in expressing the fundamental complexity of any ecosystem. Surely the stimulus to approach problems in new ways which these equations have evoked cannot be overlooked. Certainly there has been progress from the original monoclimate concept in plant ecology and zonal concept in pedology which emphasized the importance of climate almost to the exclusion of all other factors. Yet it cannot be said that all of the factors which control the development of any ecosystem have, indeed, been uncovered. We, perhaps, have only an inkling of the many and varied actions, reactions, and interactions of numerous factors which determine the nature of our biotic communities.

Thus in any study of a primary plant succession and its concomitant soil development we are confronted with the difficult questions of what are the factors that control plant and soil development and how do they act. The first question can possibly be answered with a greater degree of certainty than the

second. The five factors of Jenny and Major are undoubtedly operative in any plant and soil chronosequence and hence operative in this study of plant and soil development on the Mesabi range spoil banks. In addition, fire should also be considered as a controlling influence. The order in which these six factors are described below should not be interpreted as a ranking according to importance. There are so many interactions between these factors that it is impossible to assign any one of them as being more important than another in this chronosequence study.

ORGANISMS

The nature of the pioneer vegetation which invades any bare area is, of course, limited in a broad sense to the plants which exist in the surrounding vegetation and in a narrow sense to those species which are capable of having their disseminules transported readily by wind or animals to the bare area and which can successfully germinate and grow on that area.

In the mid-19th century, prior to extensive activity of the white man, northeastern Minnesota was covered by a conifer forest which had as its dominant components *Picea glauca*, *Pinus strobus*, *Pinus resinosa*, *Pinus banksiana*, and *Betula papyrifera* on the uplands and *Picea mariana*, *Larix laricina*, and *Thuja occidentalis* on the lowlands (Rosendahl & Butters 1928). Interspersed among the dominant trees of the uplands were small patches or scattered individuals of *Populus tremuloides*.

Perhaps the first significant human disturbance of this essentially virgin forest occurred in 1865 and 1866 when a miniature gold rush took place near Lake Vermillion, 25 mi. north of Virginia. Then, and in succeeding years, prospectors wantonly set fire to the vegetation in order to examine the underlying bed rock more easily. Without exception these attempts met with failure, and the gold fever subsided almost as quickly as it began. However, the countryside bore the scars of this futile venture for many years (Winchell 1879, Hall 1880, Wirth 1937).

Although the lumbering industry in Minnesota began as early as 1839, it was not until the early 1880's that the forests along the Mesabi range began to be harvested (Larson 1949). At first only the largest and best white pines were cut. Later, smaller and poorer pines were cut. Finally the other coniferous species were harvested also. In this process of cutting and recutting, most of the aspens were broken or cut off. The slashings left behind by the lumbermen were excellent tinder, and there was hardly a section of cutover land which was not burned over at least once if not several times. After every fire aspen suckers came up more abundantly and extensively until most of the forest land in northeastern Minnesota was covered by vast areas of almost pure aspen. By 1929, an estimated two-thirds of the total forest area in northern Wisconsin and Minnesota was occupied by aspen (Kittredge & Gevorkiantz 1929).

Completing the destruction of the virgin forest along the Mesabi range was the mining industry itself which began in 1892. Lands which had originally been purchased or leased for their timber were quickly stripped of their surface glacial till to expose the iron ore below. Villages and towns quickly sprang up all along the range due to the tremendous influx of settlers, fortune hunters, and others. Roads were built, railroads laid down, and marginal land cleared for the available timber and agricultural purposes.

Thus the present vegetation which exists along the Mesabi range is vastly different from that of a hundred years ago. Much of the land not actually utilized by man supports an essentially pioneer vegetation dominated by *Populus tremuloides* with the addition of *Populus balsamifera*, *Prunus pensylvanica*, and *Betula papyrifera* in lesser quantities. Herbaceous weed species abound along the roadsides, the edges of the mining areas, and other disturbed areas. The spoil banks, which are a result of the mining operations, are usually deposited as close to the mines as possible for economic reasons and thus, for the most part, are surrounded by this pioneer type vegetation described above.

Animals, especially birds, play an important part in this primary succession by transporting disseminules to the bare areas. Many of the species present on the spoil banks, such as *Prunus pensylvanica*, *Fragaria virginiana*, *Rubus idaeus* var. *strigosus*, and *Trifolium repens*, undoubtedly were brought there as seeds passing unharmed through the digestive tracts of birds.

Man has obviously had a profound influence on this chronosequence. The present vegetation along the Mesabi range, as indicated above, has largely developed following destruction of the native vegetation and disturbance of soil by man. And, of course, the study areas themselves are a product of civilization.

CLIMATE

According to the Thornthwaite system of classification (1948), the climate of the Mesabi range would be characterized as humid, with a moisture index of 20 (ratio of precipitation to potential evapotranspiration), second microthermal, with little or no moisture deficiency throughout the year, and a temperature-efficiency regime normal to first microthermal (summer concentration of thermal efficiency 61.6-68.0%). This would be expressed symbolically as $B_1C_2rb_1'$.

The data which are presented in graphic form in Figure 3 are from appropriate weather reports of the Virginia, Minn. station located near the center of the Mesabi range. The average annual precipitation is 27 in., of which 18 in. fall during the summer months. The temperature has varied within the 59-year period of record from 101° to -49°F. The growing season is short, averaging 108 days annually.

RELIEF

The general relief of the spoil banks along the Mesabi varies considerably. Many of the first banks

to be formed were deposited by train, which necessitated a long and gentle grade for the railroad bed along the top surface of the bank. With the later use of more mobile trucks and conveyor belts, however, the spoil banks could be built to much greater heights than before. Hence the height of the spoil banks may vary from a few to 150 ft depending on the mode of deposition, the size of the area available for dumping purposes, and the amount of material to be deposited. Possibly those banks of low elevation are more readily invaded by many kinds of disseminules than those of greater elevation.

In addition to this factor of macro-relief, micro-relief of the surfaces plays an important part during the first years of invasion by plants. Small depressions in the surface serve as areas of windblown disseminule retention and as reservoirs for the collection of precipitation. Thus on most young spoil banks, the vegetation which is present is usually confined to the micro-valleys and concavities of the surface.

PARENT MATERIAL

The glacial till, which forms the parent material of the stripping spoil banks, is of three types which vary in texture and pH: a brown sandy till, a red clayey till, and a gray or buff silty till. The first two are slightly acid in reaction, while the last is slightly alkaline or circumneutral. All three have numerous glacial stones and pebbles. The silt and clay content of the red and gray tills is relatively high, but very low in the brown till. In any stripping operation, the upper layers of till must obviously be removed before the lower layers and hence could also be deposited on the spoil bank area before the lower layers. Thus, on many stripping banks, the natural orientation of the till layers is frequently reversed, the uppermost gray till forming the basal layers of the spoil bank and the lower brown till forming the surface layers. This is important for two reasons: (1) any plant parts that might be transported in the gray till would be deeply buried under layers of sterile material in the spoil bank; and (2) the brown till, being very low in silt and clay content, is the least suitable of the three tills as a substrate for plant growth. In other banks, however, the different till layers have been intermixed in the dumping operations to such an extent that it is impossible to distinguish distinct types.

The lean ore banks of this study are composed of either cherty or slaty taconite which forms an extremely coarse-textured substrate. The amount of finely divided material is usually very low, with most of the particles averaging 3 to 6 in. in diameter. Cherty taconite is very hard and resistant to weathering, while slaty taconite is somewhat softer and less resistant. The average chemical composition of taconite is shown in Table 1.

TIME

The factor of time is, of course, the basic variable in any chronosequence study. In the stripping spoil

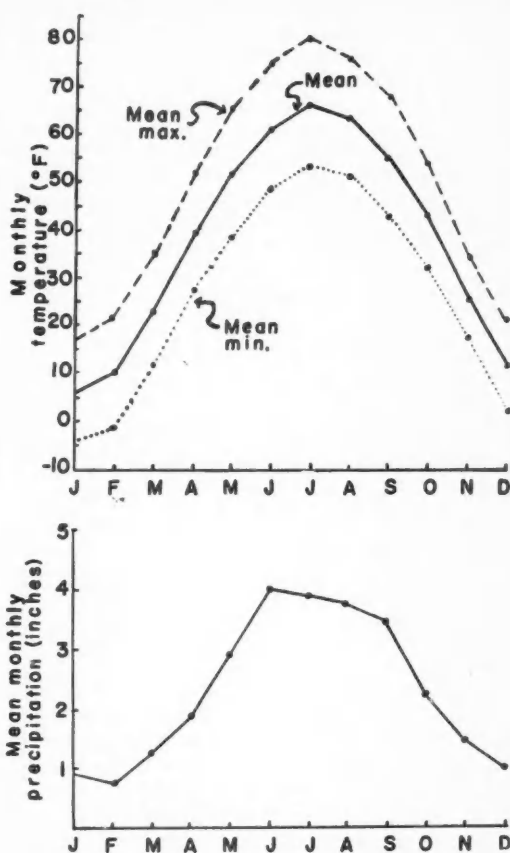


FIG. 3. Climatic data for Virginia, Minn. Based on data from 1894 to 1952.

TABLE 1. Average chemical composition of the Biwabik formation, excluding the hematite-limonite ores (Gruner 1946).

Constituent	Per cent
SiO ₂	51.0
Al ₂ O ₃	1.0
Total Fe.....	27.0
Mn.....	0.4
MgO.....	2.8
CaO.....	1.1
CO ₂	5.0
P.....	0.035
Combined H ₂ O.....	2.2

bank chronosequence, the oldest bank was 51 yrs old as compared to a 31-year old bank in the lean ore chronosequence.

FIRE

The extreme importance of fire as one of the basic factors in the formation of the existing vegetation along the Mesabi range has already been mentioned

in the discussion of organisms. It is perhaps only necessary to add the Chisholm fire of 1908, which burned about 400,000 acres of timber and destroyed the village of Chisholm (Larson 1949), as one outstanding example of the pernicious nature of this factor. As early as 1879, it was estimated that fires annually destroyed about ten times as much pine as was cut by lumbermen (Winchell 1879). However, as far as could be determined, fire has not apparently been a factor in the actual development of vegetation on the spoil banks of this region.

VEGETATION AND SOIL DEVELOPMENT

METHODS AND PROCEDURES

The summers of 1952 and 1953 were spent on the field work of this problem. Much of the first summer was spent in a general reconnaissance of the Mesabi range to ascertain the extent and possibilities of the various spoil banks. At that time it was decided to study the vegetation and soil chronosequence on the stripping spoil banks and the vegetation chronosequence alone on the lean ore spoil banks, the general absence of finely divided material on the lean ore banks prohibiting any study of soil development. Spoil banks at approximately 10-year intervals in time of deposition were selected for quantitative study. Exact locations and dates for the deposition of the spoil banks were supplied by engineers of the various mining companies and by records of the Division of Lands and Minerals of the Minnesota Department of Conservation at Hibbing. The selection of spoil banks to be studied was based on general accessibility and freedom from possible human disturbance.

Quantitative study of the woody vegetation on both types of spoil banks was done by the use of sets of nested plots arranged as follows. Trees greater than 4 in. (10.16 cm) d.b.h. (diameter at breast height) were recorded in 10 m \times 10 m plots; those less than 4 in. d.b.h. but greater than 54 in. (137.16 cm) tall and shrubs were recorded in a 2 m \times 10 m strip along one edge of each large plot; and trees less than 54 in. tall were recorded in four $\frac{1}{2}$ m \times 2 m plots located at each corner of the large plot. Height, d.b.h., and basal diameter, measured 1 in. above the soil surface, were ascertained for each tree recorded, and basal sections or increment borings were obtained from each tree for age determination. After the age of each tree had been ascertained by a ring count of the section or boring, the rate of height and basal diameter growth were calculated. A total of 10 evenly-spaced nests of plots was placed on each spoil bank with the exception of the 32-, 41-, and 51-year old stripping banks, where only 5 quadrats were used because of time limitations. Frequency, density, and dominance were calculated for each site on the basis of the data obtained from the quadrats. Frequency is equal to the percent of the quadrats occupied by a given species ranked according to the appropriate size class mentioned above. Density is equal to the average number of individuals of a given species in appropriate size classes per unit area

(100 m²). Dominance, calculated only for those trees taller than 54 in., and as here expressed, is equal to the average basal area in square inches of a given species per unit area.

The herbaceous vegetation was studied quantitatively by the use of the point-contact method. This sampling technique was first developed by Levy (1933) and is based on the general principle that a quadrat becomes increasingly more accurate as it decreases in size. A point, being the smallest possible quadrat, is, therefore, the most accurate measuring device. The sampling unit in the point-contact method is the point of a pin which is lowered on the vegetation, with the species contacted by this point being recorded. Through successive projections of this pin or other pins, a statistically sound sampling of the vegetation can be obtained. The method of recording the hits of a single pin projection varies considerably. Some workers count only hits on the base of the plant, others only the first plant hit, and still others all plants hit. While the merits of each method vary somewhat according to the vegetation being sampled, it has been shown (Tinney, Aamodt & Ahlgren 1937, Drew 1944) that greater accuracy can be obtained by recording all plants hit by the pin.

The point-contact method was developed primarily for use in grassland analysis where other methods proved cumbersome and inaccurate. However, it has been used in mixed swards and forest ground cover with a considerable degree of accuracy also. The method has the advantages of a saving in time and labor, the lack of disturbance or damage to the vegetation, and greater precision and objectivity. For a complete historical review of the point-contact method the reader is referred to Brown (1954).

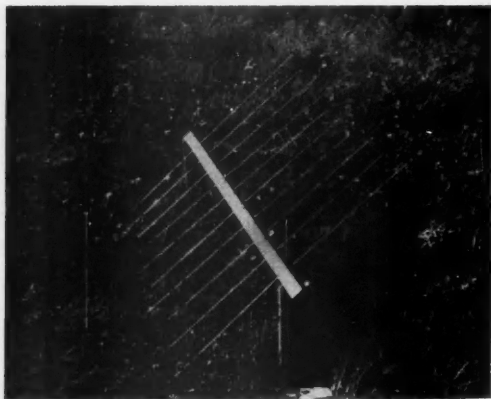


FIG. 4. Point apparatus used in the point-contact study of herbaceous vegetation.

The point apparatus used (Fig. 4) was a wooden frame supporting 10 steel pins (welding rods 36 in. long) at a height of 12 in. above the soil surface and inclined at a 45° angle to the vertical as used by Tinney, Aamodt & Ahlgren (1937). The pins were spaced at decimeter intervals on the meter-long frame. At each placement of the point apparatus

the pins were successively projected downward, and the number of contacts with each species was recorded. If the pin at ground level contacted bare substrate or litter rather than living plants, this was recorded also. A total of 20 evenly-spaced placements of the apparatus was used on each spoil bank. Since there were 10 pins in the apparatus, a total of 200 pin projections was utilized per spoil bank. The low-growing shrub, *Rubus idaeus* var. *strigosus*, was included along with the herbs, since in many instances it formed a very prominent part of the ground cover. Thus this species is recorded in the analysis of both woody and herbaceous vegetation. Frequency was calculated as the percent of the placements in which a given species was contacted at least once by a pin. Some measure of the cover of the individual species may be gained by comparing the total number of hits per species.

The point-contact study was made on all spoil banks during a one-week period in the latter part of August, 1953. This avoided the difficult problem of identification of species in the seedling stage, since all were reasonably matured by this time. In addition, the sampling of all banks at the same time of the year enable logical comparisons to be made on the amount and species composition of the herbaceous vegetation.

Scientific nomenclature of the various plants in this paper is that of Fernald (1950). Specimens of each species were collected and have been deposited in the University of Minnesota herbarium.

Three soil profile pits were dug to a depth of 15 in. on each of the stripping spoil banks where a fairly uniform vegetative cover existed. On those banks where a mosaic of woody and herbaceous vegetation was present, 3 profile pits were dug under each type of vegetation making a total of 6 pits per bank. The average depths of the A and A₀ horizon, where present, were recorded for each site. Soil volume samples were collected from each pit by means of a cylindrical brass sampler having a diameter of 3.5 cm, a length of 4.9 cm, and a volume of 47.14 cc. The soil profile was sampled at the 1 in. (2.54 cm), 4 in. (10.16 cm), and 9 in. (22.86 cm) levels with 2 volume samples being taken at each level per pit. Thus in 3 pits a total of 6 volume samples was collected at each level or a total volume of 282.84 cc of soil per level on each site. The soil samples were placed in soil moisture cans and dried as soon as possible in a drying oven at the Hibbing office of the Division of Lands and Minerals at a temperature of 65° C for 24 hours. This was done to lower the available moisture and reduce microbial activity to a minimum in the interim between collection and testing of the samples.

Soil tests were run on these samples during 1954. The samples were first dried at 105° C for 24 hours, cooled in a desiccator, and bulk density values ascertained for each sample. The soil was then screened to remove those particles greater than 2 mm in size and resealed in soil moisture cans. In tests in-

volving critical weighing of the soil sample, it was redried by the above procedure just prior to testing. The following determinations were made: mechanical analysis for sand, silt, and clay content by the hydrometer method; pH by the glass electrode method; moisture equivalent; organic carbon percentage by the dry combustion method (Piper 1942); and total nitrogen percentage by the Kjeldahl method. Each test was run in duplicate, and the average between the two results is presented in the data of this paper.

RESULTS

VEGETATION AND SOIL CHRONOSEQUENCE ON STRIPPING SPOIL BANKS

Spoil banks deposited in the following years were selected for this study (age of surface in parentheses): 1951 (2 yrs), 1940 (13 yrs), 1932 (21 yrs), 1921 (32 yrs), 1912 (41 yrs), and 1902 (51 yrs), the last being the oldest undisturbed stripping spoil bank that was found.

A general visual survey of many stripping banks along the Mesabi range revealed a rather uniform successional picture. The initial invaders or pioneer species are generally those whose disseminules are readily transported by wind or birds and mammals. These are chiefly herbaceous weed species which abound over the much disturbed landscape along the range. Simultaneously, or following shortly thereafter, aspen (*Populus tremuloides*) and frequently balsam poplar (*Populus balsamifera*) were observed as the principal woody invaders. Rapid growth and root suckering are the mechanisms by which the poplars, chiefly aspen, come to dominate the tree stratum. A ground cover consisting of a mixture of weed forbs and sod-forming grasses, chiefly *Poa pratensis*, develops.

Occasionally a few of the older spoil banks exhibit a grassland type vegetation with only isolated clumps of aspen and balsam poplar. One of the banks of this study possessed a grassland cover, and an effort was made to discover why this vegetation developed instead of aspen woodland.

The spoil banks of 1951, 1940, 1932, 1921, and 1902 illustrate succession through the aspen and balsam poplar community, while the 1912 spoil bank is considered separately as an example of succession through grassland.

Judson stripping spoil bank

This spoil bank was deposited during 1950 and 1951 and extended about 100 ft above the general land surface. The uppermost surface, which is the only one considered in the present studies, was 2 yrs old when observed. It is located in the southwest corner of Sec 20, T 58 N, R 19 W about 0.25 mi. west of Buhl and just south of U.S. Hwy 169. At the time of observation, only scattered patches of vegetation existed on the 2-year old surface. No seedlings of woody species were noted, hence no quadrats were laid down. Of the herbaceous vegetation *Trifolium repens* was the most abundant, show-

ing up as a single hit in the point-contact study (Table 2). Other isolated patches, less than 1 ft in diameter, of *Poa pratensis*, *Erigeron canadensis*, *Oenothera biennis*, *Potentilla* sp., *Chenopodium album*, and *Salsola kali* were also present but were not recorded in the point-contact study. It was noted here, as well as on other spoil banks, that the pioneer patches of vegetation are most often confined to small depressions in the surface of the bank (Fig. 5). This is undoubtedly due to the fact that the depression offers a favorable location for the retention of wind-blown seeds and moisture, the latter being one of the critical factors in the invasion of bare areas of this type.



FIG. 5. A 4-year old stripping spoil bank showing vegetation confined to small depressions in the surface.

No evidence of A_0 and A horizon development was noted in the three soil pits which were dug. Soil sample data are recorded in Table 4.

Butler Bros. No. 11 stripping spoil bank

Deposition of this spoil bank occurred in 1940, 13 yrs before this study. Its elevation above the land surface is about 40 ft. It is located in the southeast corner of Sec 32, T 57 N, R 23 W about 1.25 mi. NNW of the town of Cooley. The surface was completely covered with a ground cover vegetation consisting mainly of *Trifolium repens*, *Poa pratensis*, and *Fragaria virginiana* (Table 2). Young *Populus tremuloides* were fairly numerous, 4 being recorded in the quadrat study (Table 3). Isolated specimens of *Populus balsamifera* and *Prunus pensylvanica* were also present but, with the exception of one *Prunus* seedling, did not happen to occur in any of the quadrats.

Three soil pits were dug under the predominantly herbaceous cover. No A_0 horizon was evident but incipient A horizon development was noted to a depth of 0.5 in. (1.27 cm). The results from the soil sample tests are summarized in Table 4.

Harrison No. 1 stripping spoil bank

This spoil bank was deposited in 1932 and has an elevation of about 25 ft. It is located in the southeast corner of Sec 1, T 56 N, R 23 W, 0.25 mi. WNW of the town of Cooley. About 60% (ascertained by

TABLE 2. Point-contact data for the stripping spoil bank woodland succession including only species with greater than 10% frequency. Frequency equal to percent of 20 placements in which species was contacted.

Species	AGE OF SURFACE									
	2 yrs.		13 yrs.		21 yrs.		32 yrs.		51 yrs.	
	Hits	Freq.	Hits	Freq.	Hits	Freq.	Hits	Freq.	Hits	Freq.
<i>Trifolium repens</i>	1	5	186	95	40	65	156	100	143	75
<i>Poa pratensis</i>			124	85	363	100	86	70	94	65
<i>Fragaria virginiana</i> ...			49	45	7	25	56	80	79	95
<i>Sonchus arvensis</i> var.										
<i>glabrescens</i>			31	55	5	20	4	15		
<i>Melilotus alba</i>			31	45	177	95				
<i>Achillea millefolium</i> ...			14	30	3	10	20	40	3	15
<i>Trifolium pratense</i> ...			14	10	13	30				
<i>Cinna latifolia</i>			8	15						
<i>Solidago nemoralis</i> ...			7	20	3	15	29	40	6	20
<i>Erigeron canadensis</i> ..			5	10						
<i>Rubus idaeus</i> var.										
<i>strigosus</i>			4	10	11	30	7	15	94	75
<i>Solidago gigantea</i> var.										
<i>leiophylla</i>			4	10	3	10				
<i>Phleum pratense</i>			1	5	22	35			162	75
<i>Agropyron repens</i>					14	15				
<i>Cirsium arvense</i>					9	15			3	15
<i>Equisetum arvense</i> ...					2	10				
<i>Aster ciliolatus</i>					2	5			7	15
<i>Aster macrophyllus</i> ...							8	15		
<i>Diervilla lonicera</i> ...							7	15		
<i>Hieracium canadense</i> ..							4	10		
<i>Aralia nudicaulis</i> ...									6	20
Bare substrate.....	200	100	51	55						
Litter.....			118	90	198	100	174	100	189	100

visual inspection) of this 21-year old surface supported a woody vegetation of *Populus tremuloides*, *P. balsamifera*, and *Prunus pensylvanica*, while the remaining 40% consisted of an herbaceous vegetation consisting mainly of *Poa pratensis* and *Melilotus alba* (Tables 2 and 3).

A total of 6 soil profile pits was dug, 3 under grassland and 3 under woody cover. Slight development of the A_0 horizon was evident under both types reaching an average depth of 0.125 in. (0.31 cm) in each case. Development of the A horizon to an average depth of 1 in. (2.54 cm) was noted under both types of vegetation.

Warren stripping spoil bank

Deposition of the upper surfaces of this spoil bank occurred in 1921. The elevation of this 32-year old bank averaged 15-25 ft. It is located in the southwest corner of Sec 9, T 57 N, R 21 W, about 3 mi. west of Hibbing. Like many of the oldest spoil banks on the range, this bank was laid down by train, the old railroad bed still being visible in places on the upper surfaces of the bank (Fig. 6). Thirty-two years of vegetative development have led to a very uniform woodland community, composed chiefly of *Populus tremuloides* and secondarily *P. balsamifera*. *Betula papyrifera* and *Prunus pensylvanica* were also present as isolated specimens. Although they were not recorded in the quadrats, occasional seedlings of *Abies balsamea* were noted, which might indicate a change at some time in the future toward a more

TABLE 3. Quadrat data for the stripping spoil bank woodland succession. Freq. = Frequency, Dens. = Density, Dom. = Dominance.

Species	AGE OF SURFACE											
	13 yrs.			21 yrs.			32 yrs.			51 yrs.		
	Freq.	Dens.*	Dom.**	Freq.	Dens.	Dom.	Freq.	Dens.	Dom.	Freq.	Dens.	Dom.
Trees <54" height												
<i>Populus tremuloides</i>	20	5.0	..	80	70.0	..	40	35.0	..
<i>Populus balsamifera</i>	10	5.0	..	60	25.0	..	80	100.0	..
<i>Prunus pennsylvanica</i>	10	2.5
Trees >54" height <4" d. b. h.												
<i>Populus tremuloides</i>	20	2.0	3.70	50	6.5	9.30	100	22.0	83.05	60	9.0	66.35
<i>Populus balsamifera</i>	20	3.0	3.20	40	5.0	19.75
<i>Prunus pennsylvanica</i>	20	4.0	3.75	40	2.0	10.20
<i>Betula papyrifera</i>	20	2.0	8.35
Trees >4" d. b. h.												
<i>Populus tremuloides</i>	100	2.2	46.07	100	4.6	96.86
<i>Populus balsamifera</i>	20	0.6	13.46	20	0.2	6.63
Shrubs												
<i>Salix</i> sp.	20	3.0	..	40	3.5	..	60	7.0
<i>Rubus idaeus</i> var. <i>strigosus</i>	30	4.0	..	40	3.0	..	100	113.0	..
<i>Cornus stolonifera</i>	20	2.0	..

*Average number of specimens per 100 m².**Average basal area (inches²) per 100 m².

FIG. 6. Warren stripping spoil bank showing dense growth of aspen and balsam poplar. Railroad bed used in deposition of this bank still visible in foreground.

shade-tolerant community, provided no disturbance takes place. The ground cover was also fairly uniform, though rather sparse due to the overstory of woody species. *Trifolium repens*, *Poa pratensis*, and *Fragaria virginiana* were again the dominant species.

Three soil pits were dug under the dominant aspen cover. The average depth of the A₀ horizon was 0.25 in. (0.63 cm) and the average depth of the A horizon was 1.125 in. (2.85 cm).

Kinney stripping spoil bank

This, the oldest stripping spoil bank found, was deposited in 1902. It is located in the southwest corner of Sec 4, T 58 N, R 19 W, about 0.25 mi. southeast of the village of Kinney. This 51-year old surface, about 20 ft above the surrounding land, supported a uniform woodland community, dominated by *Populus tremuloides*, but with occasional *P.*

balsamifera and *Betula papyrifera* also present. A visual survey of the bank failed to reveal the presence of any young conifers or other more tolerant deciduous trees, presaging no immediate change in the vegetation type. The ground cover vegetation was dominated by *Phleum pratense*, *Trifolium repens*, *Rubus idaeus* var. *strigosus*, and *Poa pratensis* (Tables 2 and 3).

Three soil pits were dug under aspen cover and revealed an average A₀ horizon thickness of 0.5 in. (1.27 cm) and an A horizon depth of 1.75 in. (4.44 cm).

Sliver stripping spoil bank

Deposition of this spoil bank occurred in 1912, making the surface layers 41 yrs old at the time of observation. Its elevation is about 75 ft. It is located in the northeast corner of Sec 6, T 58 N, R 17 W, 1 mi. north of the city of Virginia. This predominantly grassland site is considered separately in the following discussion as being an exception to the normal woodland succession. The sparsity of trees is indicated in the quadrat study (Table 5) which showed no trees greater than 4 in. d.b.h. and only slight representation of aspen and balsam poplar in the other two smaller size classes. The ground cover was dominated by *Poa pratensis* and *Fragaria virginiana* (Table 6), the number of hits on the former being more than on any other site in this chronosequence.

Three soil pits were dug under herbaceous cover and 3 under the isolated clumps of aspen and balsam poplar. The average thickness of the A₀ horizon was 0.25 in. (0.63 cm) under both herbaceous and woody cover, and the average depth of the A horizon was 2.5 in. (6.35 cm) under herbaceous cover and 1.75 in. (4.44 cm) under woody cover.

TABLE 4. Results of the soil sample analyses.

Soil level	Bulk density	MECH. ANALYSIS			pH	Moisture Equivalent	% Org. Carbon	% Total Nitrogen	C/N Ratio
		% Sand	% Silt	% Clay					
Judson (2 years old)									
1".....	1.44	70.4	16.8	12.8	7.45	10.55	0.08	0.005	16.0:1
4".....	1.57	71.0	17.4	11.6	7.35	9.70	0.05	0.003	16.7:1
9".....	1.57	73.0	16.8	10.2	6.35	9.95	0.05	0.003	16.7:1
Butler Bros. No. 11 (13 years old)									
Herbaceous cover									
1".....	1.42	65.0	17.0	18.0	7.50	10.42	0.46	0.036	12.8:1
4".....	1.45	64.0	18.4	17.6	7.95	11.85	0.16	0.011	14.5:1
9".....	1.43	60.8	18.0	21.2	7.60	12.60	0.16	0.012	14.5:1
Harrison No. 1 (21 years old)									
Herbaceous cover									
1".....	1.10	71.0	19.8	9.2	6.35	11.31	0.90	0.074	12.2:1
4".....	1.37	64.2	20.0	15.8	6.70	11.61	0.25	0.018	13.9:1
9".....	1.46	46.0	26.8	27.2	6.80	18.94	0.11	0.008	13.8:1
Woody cover									
1".....	1.22	74.0	15.8	10.2	7.40	10.98	0.84	0.062	13.5:1
4".....	1.38	65.4	17.4	17.2	7.95	11.63	0.35	0.023	15.2:1
9".....	1.45	74.0	18.4	7.6	8.40	4.45	0.23	0.015	15.3:1
Warren (32 years old)									
Woody cover									
1".....	1.42	86.0	7.4	6.6	5.90	5.30	0.38	0.028	13.6:1
4".....	1.50	90.4	3.8	5.8	5.70	3.91	0.25	0.017	14.7:1
9".....	1.53	94.0	1.8	4.2	6.05	2.93	0.11	0.007	15.7:1
Sliver (41 years old)									
Herbaceous cover									
1".....	1.25	80.8	10.4	8.8	5.95	9.69	0.92	0.076	12.1:1
4".....	1.47	85.0	6.4	8.6	6.35	9.02	0.49	0.034	14.4:1
9".....	1.42	75.2	12.0	12.8	6.40	12.62	0.30	0.020	15.0:1
Woody cover									
1".....	1.25	70.4	18.0	11.6	6.85	10.65	1.05	0.079	13.3:1
4".....	1.46	70.4	16.0	13.6	7.25	10.41	0.66	0.048	13.8:1
9".....	1.48	70.8	15.4	13.8	7.45	11.73	0.27	0.019	14.2:1
Kinney (51 years old)									
Woody cover									
1".....	1.32	47.0	25.0	28.0	5.90	22.00	1.26	0.098	12.9:1
4".....	1.52	35.6	27.4	37.0	6.55	23.88	0.71	0.057	12.5:1
9".....	1.61	42.0	25.0	33.0	7.50	20.70	0.35	0.022	15.9:1

The data for rates of height and basal diameter growth of aspen and balsam poplar on all of the stripping banks showed a general increase in magnitude from the youngest to the oldest spoil bank sampled. The average annual rate of height growth of aspen was 12.3 in. (31.24 cm) on the 13-year old bank and 19.4 in. (49.27 cm) on the 51-year old bank and of balsam poplar, 15.7 in. (39.88 cm) on the 21-year old bank and 16.9 in. (42.93 cm) on the 51-year old bank. The average annual rate of basal diameter growth increased from 0.17 in. (0.43 cm) to 0.20 in. (0.51 cm) with aspen and from 0.18 in. (0.46 cm) to 0.24 in. (0.61 cm) with balsam poplar on the above mentioned sites.

DISCUSSION AND ANALYSIS OF THE DATA

Vegetation

That the nature of any primary plant succession is, to a large part, dependent on the nature of the sur-

rounding vegetation, is well illustrated by the foregoing data. As was indicated in the previous discussion of environmental factors, most of the landscape along the Mesabi range has been greatly modified by man's industrial activities to an aspen-brush type vegetation in which pioneer weed species, both woody and herbaceous, form the main cover. *Populus tremuloides* and *P. balsamifera*, both possessing light, wind-blown seeds, are the chief woody pioneer species on the stripping spoil banks. Among the herbaceous species, *Trifolium repens*, *Poa pratensis*, and *Melilotus alba* are the important invaders. These are very common roadside weeds in this area and produce abundant seed. *Trifolium* and *Melilotus* seeds are probably brought to the banks after passing through the digestive tracts of birds. Seeds of *Poa pratensis* are very light and are probably transported by wind to new areas. All three thrive under full sunlight,

TABLE 5. Quadrat data for grassland stripping spoil bank.

Species	AGE OF SURFACE		
	Freq.	41 yrs. Dens.*	Dom.**
Trees <54" height			
<i>Populus tremuloides</i>	20	2.0
<i>Populus balsamifera</i>	20	5.0
Trees >54" height <4" d. b. h.			
<i>Populus tremuloides</i>	20	3.0	17.62
<i>Populus balsamifera</i>	20	4.0	20.10
Shrubs			
<i>Rubus idaeus</i> var. <i>strigosus</i> ..	100	51.0

*Average number of specimens per 100 m².**Average basal area (inches²) per 100 m².

TABLE 6. Point-contact data for grassland stripping spoil bank.

Species	AGE OF SURFACE	
	41 yrs. Hits	Freq.
<i>Poa pratensis</i>	374	100
<i>Fragaria virginiana</i>	143	90
<i>Phleum pratense</i>	56	65
<i>Trifolium repens</i>	45	50
<i>Rubus idaeus</i> var. <i>strigosus</i>	34	45
<i>Sonchus arvensis</i> var. <i>glabrescens</i> ..	18	30
<i>Vicia americana</i>	17	10
<i>Agropyron repens</i>	9	5
<i>Achillea millefolium</i>	2	10
<i>Aster simplex</i>	2	5
<i>Solidago nemoralis</i>	1	5
Litter	190	100

and the first two, being legumes with symbiotic root nodules, are independent of soil nitrogen.

Aspen continues throughout the 51 yrs of plant development as the most prominent woody species in the woodland succession. One hundred percent frequency of aspens greater than 4 in. d.b.h. is attained in 32 yrs and maintained on the 51-year old site. Density (aver. number of specimens per 100 m²) of this same class increases from 2.2 on the 32-year old site to 4.6 on the 51-year old site. Dominance (aver. basal area in sq. in. per 100 m²) of the two largest size classes combined increases from 3.7 sq. in. on the 13-year old spoil bank to 163.21 sq. in. on the 51-year old site.

Frequency, density, and dominance of trees less than 4 in. d.b.h. but greater than 54 in. in height reaches the maximum on the 32-year old spoil bank and declines on the oldest due to the fact that most of the original pioneer trees have attained sufficient size to be included in the largest size category on the latter.

The rather high incidence of trees less than 54 in. in height on the two oldest spoil banks is probably due largely to root sucker development. Even though many of the trees on these banks have attained an age of 20 yrs or more, the age at which aspen begins to bear seeds (Zehngraff 1947), an ex-

amination of about 50 specimens less than 54 in. in height failed to reveal one which was not due to root sucker development. It is doubtful that very many of these small trees will ever reach maturity because of the rather dense shade provided by the overstory.

Of the shrubs, *Rubus idaeus* var. *strigosus* is probably the most significant, becoming increasingly more important throughout the succession as is indicated in both the quadrat and point-contact data.

Trifolium repens and *Poa pratensis*, both perennials, continue to be dominant members of the ground cover throughout the 51 yrs of woodland succession, the former attaining its maximum coverage on the 13-year old spoil bank and the latter on the 21-year old bank. *Melilotus alba*, one of the important pioneers, drops out of the successional picture by 32 yrs. This plant, unlike *Trifolium repens* and *Poa pratensis*, is a biennial and must depend on seed production and repeated seedling establishment for its continued presence in the succession. Reduction in light and available moisture by the established ground cover vegetation on older spoil banks probably makes it very difficult for this shade intolerant species to become established after the first few years of vegetation development. Other more shade tolerant perennial species, such as *Aster macrophyllus* and *Diervilla lonicera*, appear to a relatively minor extent on the 32-year old spoil bank. *Phleum pratense* apparently increases in importance through vegetative multiplication, although entirely absent on the 32-year old site, and becomes the dominant member of the ground cover on the 51-year bank.

The grassland succession, illustrated only by the Sliver stripping spoil bank, has *Poa pratensis* as its chief component. *Fragaria virginiana*, *Phleum pratense*, and *Trifolium repens* are also prominent, at least on this particular site. It should be noted, furthermore, that the species which are dominant in the grassland type vegetation are also conspicuous members of the ground cover in the woodland succession, although the degree of coverage as indicated by the total number of hits on living vegetation is less in the latter (701 on the 41-year old grassland bank and 597 on the 51-year old woodland bank). *Rubus idaeus* var. *strigosus* is likewise important on this grassland site (100% frequency, 51.0 density in the quadrat study) as well as on the older woodland spoil banks.

The sparsity of trees on the Sliver bank, plus the young age of the sampled trees (11 yrs), indicated either that conditions for establishment of aspen and balsam poplar were unfavorable or that seeds of these trees were probably absent during the critical years following deposition with only very slight invasion being possible after the herbaceous ground cover had been formed.

The seeds of aspen and balsam poplar mature early in the spring and are usually shed in late May or June. It is well known that seeds of these trees have a very short viability period in the field, varying from two to four weeks depending on local

environmental conditions. Perhaps the most critical factor in successful germination and seedling development of these species is the necessity for a continuously moist substrate surface during at least the first week of growth (Moss 1938). According to the U.S.D.A. Forest Service (1948), protection against excessive sunlight and high temperatures is also important. Presumably these factors are especially critical on the spoil banks, since, because of their elevation above the land surface, they are exposed to direct insolation and the desiccating effects of wind and high temperature. Under these conditions it may actually seem surprising that aspen and balsam poplar have invaded the spoil banks to the extent that they have. However, the surfaces of these banks are never completely flat and glacial boulders and rocks are usually scattered on the surface resulting in numerous small depressions and sheltered areas which offer micro-habitats for the retention of seeds and moisture, protection against wind, and at least partial shade. Thus on any stripping bank there should be enough micro-habitats present to provide fairly suitable germination sites. In addition, May and June, during which the seeds are shed, are months of fairly heavy precipitation. In fact June has the highest average precipitation of any month of the year. A combination of suitable micro-habitats plus adequate moisture should provide all the necessary germination requirements.

An examination of the surface of the 1912 stripping bank revealed the presence of numerous small depressions and valleys created by the dumping operations which should have offered suitable sites for aspen and balsam poplar germination. Furthermore a study of the monthly weather reports for May through August for the years 1912 through 1917 failed to reveal any adverse weather conditions which might obviously have hindered successful germination of aspen seeds. In addition, daily precipitation data from May 15 through August 15 for the years 1902 through 1932 were utilized for comparison purposes. The years 1902 through 1911 and 1921 through 1932 were assumed to be good years for poplar reproduction because of the dense poplar canopies present on the 1902 and 1921 stripping spoil banks. The years 1912 through 1920 were assumed to be poor years because of the lack of poplars on the 1912 bank. No significant differences in amount or periodicity of precipitation were evident in the data, however, when the poor years were compared with the good. As a further test, a comparison was made of only those days having greater than 0.1 in. precipitation, an arbitrarily assumed effective minimum. Again no significant differences were evident. Nor were any differences evident when the assumed minimum was raised to 0.2 in. Thus as far as could be ascertained, environmental conditions should have been favorable for aspen and balsam poplar establishment on the 1912 spoil bank. In addition, the bank had not been grazed at any time, and hence the vegetation had not been modified in this respect.

The problem seems to resolve itself to the factors of competition and poor seed crop years. The first few years following deposition of the spoil bank are undoubtedly the most critical in determining the course of the future vegetation. Within a period of 5 to 10 yrs, the surface of a stripping spoil bank becomes almost completely covered by vegetation, generally a mixture of small poplar saplings and herbaceous weeds. However, if during this period of time, the seed crops of the poplars in the adjacent areas were very poor, or if, for some reason not apparent in the weather data, free water were not available over a sufficiently long time to allow establishment, chances would be poor for successful invasion of any bare area by these species. And once an herbaceous cover had been established, the opportunity for invasion by aspen would be lost, for competition for surface moisture and light by the existing vegetation would probably preclude successful germination and growth of the poplars.

According to the U.S.D.A. Forest Service (1948), good aspen seed crops are produced, on the average, every 4 or 5 yrs with only poor or fair crops in the intervening years. Unfortunately seed crop records have been kept only during recent years, but it is conceivable, and probable, that the years 1912 through 1917 were years of poor seed production. Under such conditions the chances for invasion of the spoil bank by aspen would have been very poor.

The data for rates of height and basal diameter increase of aspen and balsam poplar on all of the stripping banks would seem to indicate a general improvement in spoil bank site quality with aging of the surfaces. This trend is indicated graphically in Figure 7 in which height and age of each aspen are plotted upon a background of the site quality curves worked out by Kittredge & Gevorkiantz (1929). Unfortunately no one has published data for site quality of balsam poplar, hence this species could not be similarly plotted. The youngest aspens plotted fall below even the poorest site quality curve. With increase in age of the trees and hence age of the surface, however, a definite improvement seems to be evident, with most of the oldest trees falling in the poor to medium and medium to good areas of the graph. However, it is probable that this trend is more apparent than real, as the following discussion of the soil will indicate.

Soil

The clay fraction is the most important component of the mineral soil, both from a chemical and physical standpoint. With increase in clay content, water-holding capacity and base exchange capacity of the soil are increased, each of extreme importance in plant growth and nutrition. On all of the stripping sites examined the percentage of clay particles was very low with the exception of the 51-year old site. And as can be seen in Figure 7, it is this site which supports the best growth of aspen. Thus the better site quality of this spoil bank may possibly be due

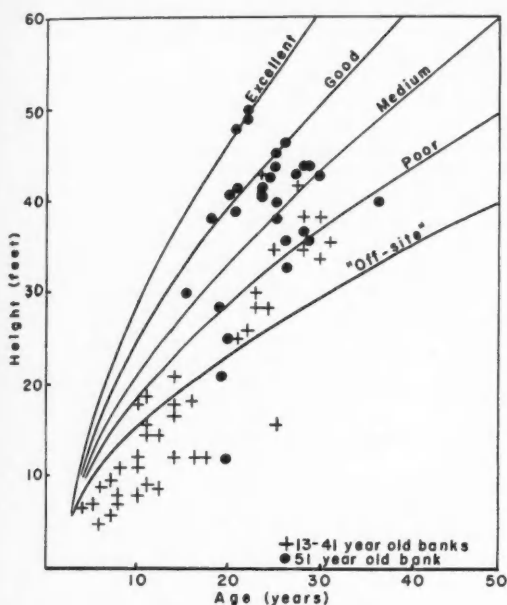


Fig. 7. Height growth in relation to age of aspen on all stripping spoil banks plotted upon a background of site quality. (Site quality graph derived from Kittredge & Gevorkiantz 1929.)

largely to its inherent high clay content rather than to improvement with time. If one ignores the loci plotted on the graph for this spoil bank, it will be seen that the trend toward site quality improvement is much less pronounced. The slight improvement in site quality with time which is still evident is probably due to increase in organic matter and nitrogen of the soil. Two of the important herbaceous pioneer species, *Trifolium repens* and *Melilotus alba*, are symbiotic nitrogen-fixing legumes, which must increase the nitrogen supply in the substrate to a much greater extent than would just the simple decomposition of non-fixing species.

Wilde & Pronin (1949) have shown that site quality for aspen in central Wisconsin is dependent to a large extent on the depth of the ground water table and the content of organic matter in the soil. Where depth to the water table is very great and organic matter content low, the site quality is very poor. These two factors are possibly controlling influences on the site quality of the stripping spoil banks also. The soil studies have shown that these banks are very low in organic carbon (Table 4). And certainly the depth to the water table must be very great, since many of the banks extend at least 50 ft above the general elevation of the land. When one considers these unfavorable characteristics in addition to the low colloidal fraction content of most of the stripping material, it is not surprising that the site quality of the younger banks is very poor.

The soil profile data are plotted graphically in

Figure 8 and show a uniform trend in increase in thickness of the A_0 horizon to 0.5 in. (1.27 cm) at the end of 51 yrs. Both herbaceous and woody cover sites were sampled on the 21- and 41-year old spoil banks. As indicated by the data, there were no apparent differences in A_0 horizon thickness as far as cover conditions are concerned. A noticeable difference, however, occurred in the depth of the A horizon. On the 21-year old bank the depth of the A horizon was 1 in. (2.54 cm) under both cover types, but on the 41-year old bank the A horizon extended to a depth of 1.75 in. (4.44 cm) under woody cover and 2.5 in. (6.35 cm) under herbaceous cover. This would seem to indicate that A horizon development is rather constant during the first 20 yrs or so of soil development regardless of cover type, but dependent to some extent on cover thereafter, developing to a greater depth under herbaceous cover than woody. This would be logical, since a large portion of the organic remains contributed by herbaceous plants to the soil is in the form of roots and rhizomes already in the soil, while most of the organic remains of woody plants is in the form of leaf litter which falls on the soil surface.

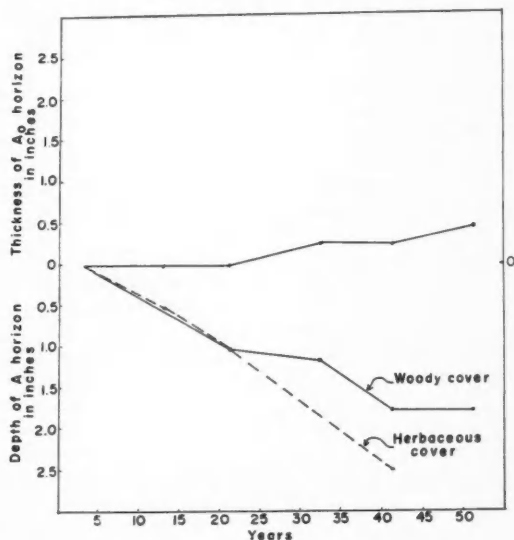


Fig. 8. Increase in thickness of A_0 horizon and depth of A horizon with time.

The mechanical analysis data of the soil samples (Table 4) show the very coarse nature of the substrate on all stripping spoil banks with the exception of the 51-year old bank where a relatively high percentage of silt and clay was found. The stripping spoil banks are usually composed of three kinds of glacial till (see discussion of parent material under environmental factors) which vary in sand, silt, and clay content and which are intermixed haphazardly during the process of deposition of the bank. Thus any trend toward relocation of silt and clay particles

from the surface layers to lower levels in the soil (incipient B horizon development) would be masked by the inherent variations which exist in the soil system due to this intermixture. Moreover, it is extremely doubtful whether B horizon development would be noticeable, and no development is evident in the data, even on the 51-year old spoil bank in uniform substrate conditions. Tyner, Tryon & Galpin (1955) found no definite B horizon development on spoil banks in West Virginia which were much older, ranging in age from 72 to 131 yrs. Crocker & Major (1955), working on morainic deposits in Alaska, found no evidence of B horizon development on 150- to 200-year old glacial till.

This same factor of non-uniformity in the substrate makes any conclusions regarding pH change with time somewhat debatable. The parent materials of the stripping banks vary in reaction from slightly alkaline (gray till) to slightly acid (red and brown tills), and an intermixture of these tills at the time of deposition creates conditions of varying pH throughout the bank. The pH values given in Table 4 do, however, indicate a noticeable trend toward more acidic conditions at the 1 in. level as compared to the 4 and 9 in. levels as the age of the spoil banks increases. Thus on the 51-year old bank the pH at 1 in. is 5.9 and at 9 in., 7.5. The question remains as to how much of this difference is due to actual acidification of the soil and how much is due to inherent variations in pH. If it can be shown that these 9 in. of soil are composed of the same till type, it should be reasonable to assume that the pH of this 9 in. profile was about the same throughout at the time of deposition. Furthermore, the chances are slight that the pH at the 9 in. level would have changed appreciably over a period of 51 yrs. That at least the surface 9 in. of soil are composed of the same till type would seem to be indicated by the mechanical analysis data which show rather constant sand, silt, and clay percentage values at the three levels sampled. Furthermore, visual inspection of the profile showed no apparent differences in till color (with the exception of the darkened A horizon) or quality to a depth of at least 15 in. It is, therefore, probable that the difference in pH between 5.9 at the 1 in. and 7.5 at the 9 in. levels represents a fair approximation of the amount of acidification which has taken place over a period of 51 yrs.

The data for moisture equivalent of the soil samples show, as would be expected, a close correlation with clay percentage values. Some slight increase may be noted, which may be due to organic matter, on the 51-year old site where the 1 in. level sample with a clay content of 28% had a moisture equivalent of 22% and the 9 in. level sample with a greater clay content of 33% had a moisture equivalent of only 20.7%. Bulk density values, though quite constant for all samples, are somewhat lower at the 1 in. depth than at the 4 and 9 in. depths, especially on the older banks, which may indicate that the increase in organic matter content at the 1 in. level is significant.

However, lack of additional corroborating data and the possibility of experimental error preclude any definite statement.

The data for organic carbon and nitrogen can be dealt with in a more positive manner since presumably the carbon and nitrogen content of raw glacial till should be practically zero at the time of deposition of the spoil bank regardless of till type. If one disregards the data from the 32-year old Warren stripping spoil bank, which indicate that both carbon and nitrogen* were very low, a uniform trend toward increased percentages of both elements with time is evident, especially at the 1 and 4 in. depths. At the 1 in. depth, organic carbon increases from 0.08% on the 2-year old site to 1.26% on the 51-year old site. Total nitrogen increases from 0.005% to 0.098% at this same depth. Graphic summaries of the data, excluding the 32-year old site, for carbon and nitrogen content are presented in Figures 9 & 10. On the 21- and 41-year old sites, where both cover types were sampled, the mean value between the herbaceous and woody cover data has been used in each figure for ease of representation. While there are some differences in the data for the two cover types on these sites, they do not appear to be biologically significant or directional, the percentage of carbon and nitrogen under woody cover being lower than herbaceous cover on the 21-year old site but higher on the 41-year old site.

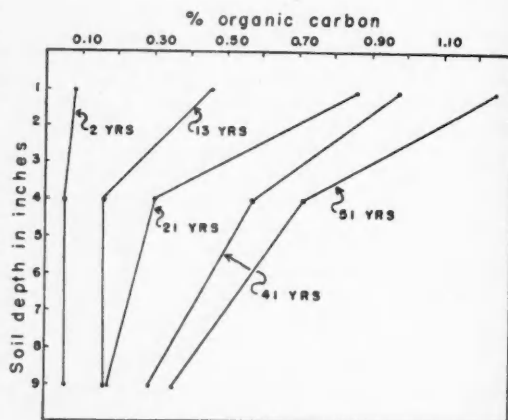


FIG. 9. The distribution of organic carbon in stripping spoil bank soils.

The carbon-nitrogen ratio of soils in the temperate regions usually approaches a value of 10 (Robinson 1936). Lutz & Chandler (1946), however, consider a value of 20 to be more common in forested soils. The data obtained in this study apparently indicate a trend toward a ratio value of 10, especially in the upper soil levels. A graphic summary of the

* The low values for carbon and nitrogen on the 32-year old Warren bank may be due to rapid leaching by percolating water. The silt and clay percentages of this site are extremely low. Hence the infiltration capacity may be conversely very high and leaching fairly rapid.

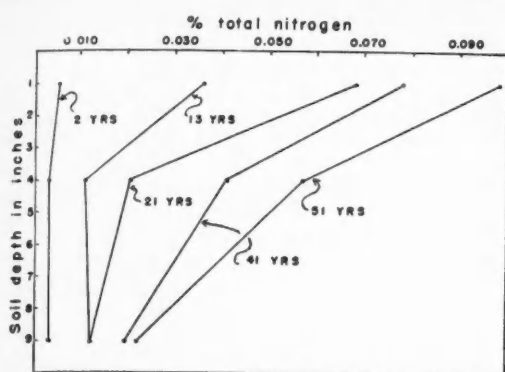


FIG. 10. The distribution of total nitrogen in stripping spoil bank soils.

C/N ratio data at the 1, 4, and 9 in. levels under both herbaceous and woody cover is presented in Figure 11. A general decrease in the ratio of carbon to nitrogen is evident at all levels. It is also apparent that the initial decrease is more rapid under herbaceous cover than woody cover. At the 4 and 9 in. levels, the ratio appears to vary without any definite pattern following this initial decrease, although a further general decrease in the ratio value at the 4 in. level under woody cover is evident. With this one exception, the data at the 4 and 9 in. levels are too inconsistent to warrant any definite conclusions.

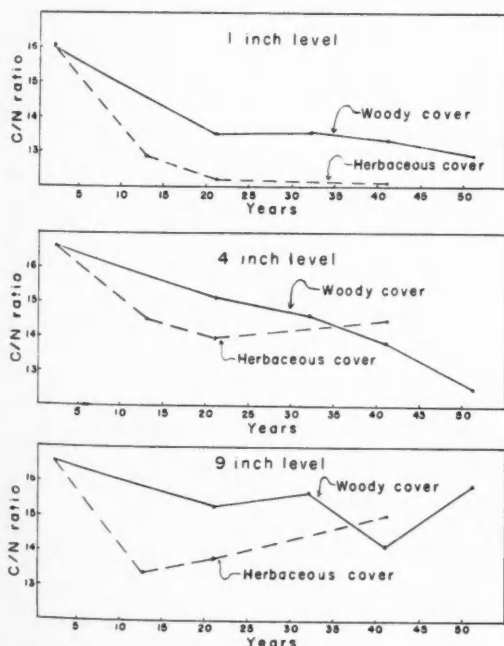


FIG. 11. Carbon-nitrogen ratios at the 1-, 4-, and 9-inch levels of the stripping spoil banks.

At the 1 in. level, the ratio is consistently lower under herbaceous cover than woody cover. The more rapid decrease of the C/N ratio and its consistently lower value at the 1 in. level under herbaceous cover are probably due to the high incidence of *Trifolium repens* and *Melilotus alba*, both nitrogen-fixing legumes, during the first few years following deposition of the spoil bank and the continued high incidence of the former throughout the 51 yrs of herbaceous cover development. Crocker & Major (1955), in their chronosequence study of glacial deposits in Alaska, obtained C/N ratios of 13-15 during an alder thicket stage of plant development. The conspicuous plant species of this stage were *Dryas* spp., *Shepherdia canadensis*, and *Alnus crispa*, all believed capable of nitrogen-fixation. With decline of the alder stage and development of the spruce forest, C/N ratios increased rapidly to 30 or more. Thus it is probable that a high incidence of nitrogen-fixing species in the plant cover effectively lowers the C/N ratio.

VEGETATION CHRONOSEQUENCE ON LEAN ORE BANKS

Lean ore spoil banks deposited in the following years were selected for this study: 1951 (2 yrs old), 1940 (13 yrs), 1930 (23 yrs), and 1922 (31 yrs), the last being the oldest undisturbed lean ore bank found.

In its general trends, the developmental sequence on the lean ore banks is similar to that on the stripping banks. Aspen and balsam poplar are again the dominant woody species, while the herbaceous ground cover, though very sparse and patchy, is composed of many of those species important in the stripping bank succession. Beyond these gross similarities, however, there are definite and important differences, both in quantity and quality, which will be pointed out in the following discussion. Such differences are, of course, to be expected since the lean ore substrate is so drastically different from the glacial till of the stripping banks (see discussion of parent material).

The relative abundance of woody plants on the lean ore banks at first seemed surprising because of the extremely coarse nature of the substrate. The size range of the taconite particles varied from finely divided material to boulders 2 ft in diameter, with the average being particles 3 to 6 in. in diameter. However, this type of substrate is probably quite favorable for seed germination, perhaps even more so than glacial till, because of the extremely numerous micro-habitats offered on the very rough surface. Whatever finely divided material is present collects in the cracks and crevices between the coarse particles. And it is in such places that wind-blown seeds collect also. Seed germination is probably quite successful since moisture would be retained in these micro-habitats, and the coarse material would offer at least partial shade and protection against wind desiccation and high temperatures.

The distinct lack of a complete ground cover vegeta-

tion on even the oldest lean ore banks undoubtedly favors invasion by woody plants also, since competition for light and moisture by herbaceous vegetation is never a problem regardless of the age of the spoil bank. Hence the opportunity for germination and successful establishment is spread over a long time period.

Webb lean ore spoil bank

The upper surface of this lean ore bank (Fig. 12), 100-125 ft in elevation, was 2 yrs old, deposition of the bank occurring in 1949-51. It is located in the northeast corner of Sec 6, T 57 N, R 20 W, just west of the Webb mine offices near Hibbing. The lean ore, primarily cherty taconite, which composed this bank was of a very coarse nature, most of the particles being 1 to 3 in. in diameter. No seedlings of woody species were evident, and only occasional specimens of *Silene acaulis*, a common roadside weed in this particular area, were encountered in the visual inspection of the surfaces. None of these, however, was contacted by pins in the 20 placements of the point apparatus (Table 8).



FIG. 12. General view of Webb lean ore spoil bank. Telephone pole and road in foreground provide some measure of scale.

Harrison No. 7 lean ore spoil bank

The Harrison No. 7 bank was deposited in 1940, making the surfaces 13 yrs old at the time of observation. It is located in the northwest corner of Sec 6, T 56 N, R 22 W, one mile WSW of Nashwauk. Like the preceding Webb bank, the cherty taconite of this bank is extremely coarse and hard, the average particle size being 5 to 6 in. in diameter. However, the height of the Harrison is only 3 to 5 ft above the general elevation of the surrounding area. Thus the chances for invasion of this lean ore by plants may be more favorable in this respect. A rather prolific growth of small trees was present, dominated by *Betula papyrifera*, and with the following species in decreasing proportion: *Populus tremuloides*, *P. balsamifera*, and *P. grandidentata* (Table 7). However, the trees were stunted, frequently deformed, and very susceptible to insect and fungal attack as evidenced by the brown discoloration of the wood and the presence of fungal conks and cankers and insect burrows. Of the 4 trees mentioned above,

the 3 species of *Populus* seemed to be the most deformed and diseased, while *Betula* was affected to a somewhat lesser degree. These poor growth qualities of the poplars were characteristic on all coarse lean ore banks observed. An experimental fertilizer study to be described later was conducted to try to discover why these trees grew so poorly.

In addition to these angiosperm tree species, scattered young *Pinus resinosa* and *P. banksiana* and occasional *Abies balsamea* seedlings were noted, but these failed to be recorded in the quadrat study. Of the shrubs, *Salix* sp. had the highest frequency, being recorded in 70% of the quadrats.

Herbaceous cover was extremely sparse, a total of only 50 hits being recorded on living vegetation in the point-contact study (Table 8). Characteristic of this and many other lean ore banks was the presence of *Polytrichum juniperinum* and *Cladonia* sp. growing commonly right on the surface of taconite rocks.

Warren lean ore spoil bank

Deposition of this bank occurred in 1930, an age of 23 yrs being assigned to the upper surfaces at the time of study. It is located in the southeast corner of Sec 9, T 47 N, R 21 W, adjacent to the Warren stripping spoil bank described previously, and has about the same elevation, 15 to 25 ft. The lean ore material of this bank is chiefly slaty taconite with an admixture of cherty taconite in spots. The texture of the substrate is again coarse, though not to the extent of the Harrison. The average particle size was about one-half to one inch in diameter. *Populus tremuloides* was the most common woody species, attaining a frequency of 60% (Table 7). *Populus balsamifera*, *Pinus banksiana*, and *Betula papyrifera* were also present but to a lesser extent. The growth characteristics of aspen and balsam poplar were the same as on the Harrison lean ore bank, with most of the trees presenting a stunted and deformed appearance.

The results of the point-contact study (Table 8) indicate the extreme sparsity of ground cover vegetation, a characteristic of practically all lean ore banks. Only *Fragaria virginiana* and *Cladonia* sp. were recorded in more than 15% of the placements and no species in more than 20%.

Hill-Annex lean ore spoil bank

This bank, located in the southwest corner of Sec 6, T 56 N, R 23 W, one-quarter mile NW of Calumet, was deposited in 1922. Its average elevation is 30 to 35 ft. In contrast to the other lean ore banks studied, the lean ore of this bank was a mixture of finely divided ore and cherty taconite with the finely divided ore predominating. *Populus tremuloides* was again the dominant tree species on this 31-year old surface, attaining a frequency of 30% in the largest size class and 100% in the second size class (Table 7). *Populus balsamifera*, *Prunus pensylvanica*, and *Betula papyrifera* were also recorded in the quadrat study but only to a relatively minor extent. A complete

TABLE 7. Quadrat data for the lean ore spoil bank succession.

Species	AGE OF SURFACE								
	13 yrs.			23 yrs.			31 yrs.		
	Freq.	Dens.*	Dom.**	Freq.	Dens.	Dom.	Freq.	Dens.	Dom.
Trees <54" height									
<i>Populus tremuloides</i>	90	162.5
<i>Populus balsamifera</i>	80	62.5
<i>Betula papyrifera</i>	40	10.0
Trees >54" height <4" d. b. h.									
<i>Populus tremuloides</i>	40	2.5	2.90	60	4.0	6.10	100	27.0	63.50
<i>Populus balsamifera</i>	30	1.5	2.35	30	1.5	0.90	30	9.5	8.55
<i>Betula papyrifera</i>	50	4.0	3.50	10	0.5	1.55
<i>Populus grandidentata</i>	20	1.0	0.55
<i>Pinus banksiana</i>	20	1.0	1.95
<i>Prunus pensylvanica</i>	10	1.0	2.40
Trees >4" d. b. h.									
<i>Populus tremuloides</i>	30	0.4	14.20
Shrubs									
<i>Salix</i> sp.	70	14.0	20	1.0	10	1.0
<i>Rubus idaeus</i> var. <i>strigosus</i>	20	1.0	30	16.0
<i>Salix bebbiana</i>	30	2.5

*Average number of specimens per 100 m².**Average basal area (inches²) per 100 m².

TABLE 8. Point-contact data for the lean ore spoil bank succession.

Species	AGE OF SURFACE							
	2 yrs.		13 yrs.		23 yrs.		31 yrs.	
	Hits	Freq.	Hits	Freq.	Hits	Freq.	Hits	Freq.
<i>Polytrichum juniperinum</i>	16	45	3	10	2	5
<i>Melilotus alba</i>	16	10	14	25
<i>Fragaria virginiana</i>	6	15	10	20	19	40
<i>Achillea millefolium</i>	3	15	1	5
<i>Sonchus arvensis</i> var. <i>glabrescens</i>	3	10	1	5
<i>Cladonia</i> sp.	2	5	5	20	2	5
<i>Poa pratensis</i>	1	5	2	10	40	35
<i>Solidago nemoralis</i>	1	5	5	15
<i>Cinna latifolia</i>	1	5	6	20
<i>Hieracium canadense</i>	1	5	1	5
<i>Trifolium repens</i>	8	10
<i>Phleum pratense</i>	44	35
<i>Artemisia caudata</i>	5	10
<i>Rubus idaeus</i> var. <i>strigosus</i>	4	5
<i>Cirsium arvense</i>	3	5
Bare substrate	200	100	167	100	185	100	82	60
Litter	19	15	15	35	107	70

survey of the bank revealed the presence of only one specimen of *Pinus resinosa*, the only coniferous species found on this site.

Although aspen and balsam poplar again showed evidence of fungal and insect attack, the general form or habit of the trees suggested better growing conditions than on the previous lean ore banks. The boles of the trees were straighter, and the heights of the trees were such as to suggest a much faster growth rate. This visual inference was confirmed in the study of the rates of height and basal diameter increase. The average rate of height growth of aspen was found to be 13.2 in. (33.53 cm) per yr as compared to 5.3 in. (13.46 cm) and 6.1 in. (15.49 cm) on the previous two lean ore banks. Balsam poplar had a height growth rate of 13.5 in. (34.29 cm) as compared to 4.0 in. (10.16 cm) and 5.0 in. (12.70 cm). The rates

of basal diameter increase showed a similar trend, with aspen having an annual increase rate of 0.16 in. (0.41 cm) as compared to 0.11 in. (0.28 cm) and 0.10 in. (0.25 cm), and balsam poplar 0.14 in. (0.36 cm) as compared to 0.08 in. (0.20 cm) and 0.1 in. (0.25 cm).

The ground cover was again sparse, although not to the extent of the previous lean ore banks studied. *Phleum pratense* and *Poa pratensis* had the greatest number of hits, 44 and 40 respectively, but a frequency of only 35% for each (Table 8). *Fragaria virginiana*, with only 19 hits, had a higher frequency of 40%.

DISCUSSION AND ANALYSIS

As in the stripping spoil bank succession, aspen was the dominant woody species throughout the lean ore vegetation chronosequence. However it attained a frequency value of 30% in the largest size class and 100% in the intermediate size class on the 31-year old lean ore site as compared to 100% frequency in both size classes on the stripping bank site of identical age. Balsam poplar, though present on all 3 older sites, never attained a frequency greater than 30%. *Betula papyrifera* played a somewhat more prominent role in the lean ore succession than in the stripping succession, attaining higher frequency, density, and dominance values than aspen on the 13-year old site, but being present to only a minor extent on the 2 older sites. *Prunus pensylvanica* and *Populus grandidentata* were present only to a limited extent throughout the observed succession. The almost ubiquitous presence of coniferous species, especially *Pinus resinosa* and *P. banksiana*, on the lean ore banks is of interest, since they were, for the most part, entirely absent from the stripping spoil bank sequence. In a visual survey of many stripping banks, including some which were adjacent

to lean ore bank with pines present, not a single specimen of either pine species and only occasional *Abies balsamea* were ever noted. Though never prominent in the lean ore vegetation, this distinctive and apparent confinement of the two pines to the lean ore succession is worthy of mention. Possibly the paucity of competition for nutrients, available moisture, and sunlight is a factor favoring development of the conifers on the lean ore, but until we know more of the life history of these species, this must remain as only speculation.

The poor site quality of lean ore for aspen growth is shown in Figure 13, where height and age of each aspen recorded in the two largest size classes in the quadrat study are plotted upon a background of site quality curves. Practically all of the trees thus plotted fall below the poorest site quality curve, with those on the coarse lean ore being furthest below it. This shows not only the poor site quality of lean ore in general, but also indicates that the finely divided ore perhaps offers a somewhat more suitable site than the coarse ore. In fact if one compares this graph with Figure 7 showing the same kind of data from the stripping banks, the loci plotted for trees on the finely divided ore do not fall very far below the loci plotted for the stripping banks, excluding the 51-year old site.

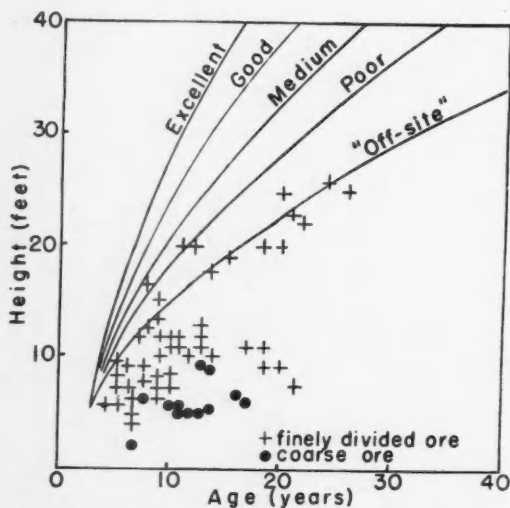


FIG. 13. Height growth in relation to age of aspen on lean ore spoil banks plotted upon a background of site quality. (Site quality graph derived from Kittredge & Gevorkiantz 1929.)

As a test of this apparent difference in site quality due to the coarseness or fineness of the ore, the rate of height and basal diameter increase for each aspen and balsam poplar recorded on the 13- and 23-yr old coarse lean ore banks was plotted against similar data for the 13- and 21-yr old stripping banks (Fig 14). Though the data are sparse, there is, none-the-less,

a distinct grouping of the loci into two portions of the graph. Rates of height and basal diameter increase on the coarse lean ore are definitely lower than the rates on stripping banks of comparable age. However, when one plots similar data from the 31-year old finely divided lean ore along with the data from the 31-year old stripping site, as is done in Figure 15, no such grouping is evident but rather an intermingling of the loci. In fact some of the loci for the finely divided lean ore are considerably higher than any for the stripping bank. Thus it is probable that the physical quality of the coarse lean ore is

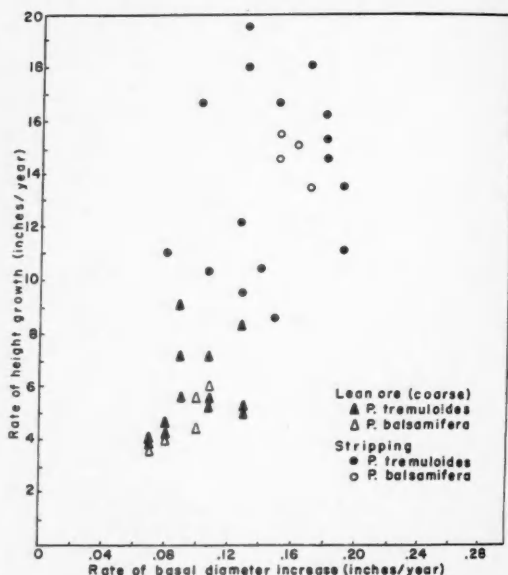


FIG. 14. Rates of height and basal diameter increase for aspen and balsam poplar on the 13- and 23-year old lean ore and 11- and 23-year old stripping banks.

a limiting factor in growth rates, at least as far as aspen and balsam poplar are concerned.

Whereas *Rubus idaeus* var. *strigosus* is the most prominent shrub in the stripping succession, it apparently is never present to any great extent on lean ore banks. Species of *Salix* are quite common to both successions, however.

The most distinguishing feature of the herbaceous vegetation on lean ore sites is its sparseness. Even on the 31-year old finely divided lean ore bank where the herbaceous vegetation was somewhat more abundant, the total number of hits on living vegetation (141) was less than half the total number of hits (377) on the stripping bank of the same age where the ground cover was even rather sparse due to the shading effect of the overstory. According to mining engineers, the finely divided ore of this bank contained a very high content of sulphur, and hence the toxic effects of the high sulphur and iron content of the ore may be the limiting factor in the growth of the herbaceous vegetation. However, it seems

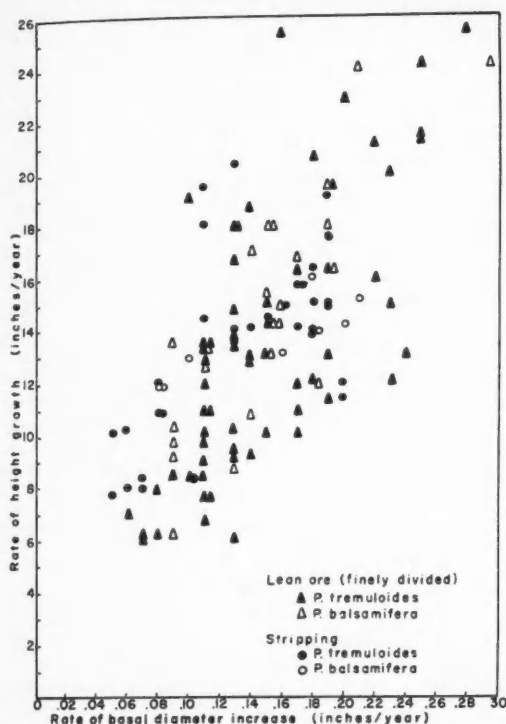


FIG. 15. Rates of height and basal diameter increase for aspen and balsam poplar on the 31-year old lean ore and stripping banks.

odd that these effects, if indeed they are present, should be manifest on the herbaceous vegetation and not the woody vegetation.

In general, it may be said that the herbaceous species which are prominent in the stripping succession are also the most common species in the lean ore succession. *Melilotus alba*, *Poa pratensis*, *Fragaria virginiana*, and *Phleum pratense*, 4 of the 5 most conspicuous herbaceous members of the stripping banks, are the most abundant members of the lean ore cover. The fifth, *Trifolium repens*, is practically absent from the lean ore succession, appearing only on the 23-year old Warren bank. *Polytrichum juniperinum* was infrequently observed on occasional stripping banks, but it occurred frequently, and *Cladonia* sp. occurred exclusively, in the lean ore succession.

A comparison of the number of hits on litter and bare substrate for both types of surfaces adds further evidence confirming the distinct lack of a complete vegetation cover on the lean ore banks. At the end of 21 yrs of vegetation development on stripping banks not a single hit was recorded on bare substrate and 198 were recorded on litter. However, even after a longer period of 31 yrs on the lean ore banks, 82 hits were still recorded on bare substrate and only 108 on litter.

FERTILIZER EXPERIMENTS

METHODS AND PROCEDURES

Since available nitrogen and possible phosphorus, potassium, and microelements were suspected to be critical factors in determining the rate of plant growth and hence in the whole progress of these primary successions on spoil banks, a series of fertilizer experiments was worked out and put into operation during 1953. Aspen was selected as the test species, since it was common to both stripping and lean ore substrates and great enough in numbers to permit adequate selection of suitable individuals for the experiments. The Hoyt stripping spoil bank, located 1 mi. west of Hibbing, was selected as a typical stripping site, and the Albany lean ore bank, 2 mi. east of Hibbing, was selected as a typical coarse lean ore site. The stripping bank was deposited in 1943 and the lean ore bank in 1936. Six experimental stations were set up on each substrate. At each station 7 aspen trees were selected, each about 4 to 5 ft tall and situated at least 30 ft apart and arranged, more or less, in a circle. All other trees within a radius of 10 ft of the selected individuals were cut off within 2 in. above the soil surface to reduce the factor of competition as much as possible. Most of these were root suckers shoots, but it would have been impossible to ascertain whether or not these were from the same root system as the test tree without damaging the root system.

The fertilizer treatments were applied in April, 1953 before the start of that year's growing season. Two of the selected trees at each station served as controls, while the remaining 5 were given various fertilizer treatments. These treatments are summarized in Table 9. A circle with an area of one milacre (3.87 ft radius) was inscribed around each tree, including the controls, and all other living vegetation within that circle removed. The fertilizer was then broadcast manually within the circle and a metal band affixed to the tree indicating the treatment applied. No fertilizer was applied to those trees serving as controls.

During the last week of August, 1953, by which time the terminal buds for the following year were formed, the lateral branches (about 8 or 9 per tree) were harvested so as to include not only the 1953 growth but also that of the preceding year, 1952. The terminal leader of the test tree was not utilized in this study, since its rate of elongation is frequently greatly in excess of the lateral branches. The amount of growth for 1953 was measured from the latest set of bud scale scars on each twig to the base of the terminal bud, while the 1952 growth was measured as the distance between the latest two sets of bud scale scars.

RESULTS AND ANALYSIS

These measurements have been summarized in Table 10 which represents the combined data of all 6 stations on each of the 2 spoil banks. The striking difference in absolute growth of the unfertilized con-

TABLE 9. Fertilizer treatments applied to milacre surfaces about individual aspens on stripping and lean ore substrates. Nitrogen where included is equal in amount throughout.

Element	Compound applied	Weight in grams per milacre plot
N.....	NH ₄ NO ₃	90.7*
PK.....	0-20-20 commercial fertilizer	90.7
NPK.....	NH ₄ NO ₃ + 0-20-20	181.4
T (trace).....	Mixture of	185.0
Cu.....	CuSO ₄	23.0
Mn.....	MnSO ₄	45.5
Mg.....	MgSO ₄	59.0
Zn.....	ZnSO ₄	11.5
B.....	Na ₂ B ₄ O ₇	23.0
Fe.....	FeSO ₄	23.0
NPKT.....	NH ₄ NO ₃ + 0-20-20 + trace mixture	366.4

*Equivalent to 66 lbs. N per acre.

trol twigs on the 2 sites is an excellent indication of the difference in site quality between glacial till and coarse lean ore mentioned earlier in this paper.

TABLE 10. Results of the fertilizer experiments on aspens on the spoil banks; data for all six stations combined.

Treatment	Total number twigs measured	Total growth of all twigs in inches		Avg. growth rate inches/year		% increase of 1953 growth over 1952
		1952	1953	1952	1953	
Stripping Bank						
Control.....	98	742.9	719.0	7.6	7.3	- 3.22
N.....	52	319.5	437.3	6.1	8.4	36.87
PK.....	46	283.3	336.2	6.2	7.3	18.67
NPK.....	48	250.4	403.5	5.2	8.4	61.14
T.....	45	276.4	256.8	6.1	5.7	- 7.09
NPKT.....	54	387.4	495.3	7.2	9.2	27.85
Lean Ore Bank						
Control.....	90	176.7	266.9	2.0	3.0	51.05
N.....	39	111.1	184.2	2.9	4.7	65.80
PK.....	52	117.6	220.7	2.3	4.2	87.67
NPK.....	45	84.9	300.9	1.9	6.7	254.42
T.....	49	83.7	120.9	1.7	2.5	44.44
NPKT.....	61	156.4	380.8	2.6	6.2	143.48

Even during 1953, when the lean ore controls showed an increase over 1952 and the stripping controls a slight decrease, the average twig growth rate of the lean ore controls was still less than half that of the stripping controls.

On the stripping site, the 12 control trees in 1953 showed a decrease in twig growth rate from 1952 of 3.22%. All of the fertilizer treatments, with the exception of the trace element application without N, P, or K, showed a definite increase in twig growth rate. The NPK treatment, with an increase of 61.14%, was the most effective. However, the addition of the trace elements to the NPK tended to decrease the effectiveness of the application. Since the trace element treatment alone also showed this inhibitory effect (-7.09%), it is possible that one

or more of the trace elements was present in amount toxic to the growth of the aspens.

On the lean ore site, the control trees in 1953 showed an increase in growth rate over 1952 of 51.05%. All of the fertilizer treatments, with the exception of the trace element mixture, increased the growth rate to a greater extent than that exhibited by the controls. NPK was again the most effective treatment with an increase of 254.42% over the 1952 growth. The apparent inhibitory effect of the trace element mixture is again evident, decreasing the effectiveness of the NPK application by more than 100% and having an increase value of only 44.44% when applied alone as compared to 51.05% in the control.

These experiments were not designed to show specific deficiencies in either substrate but rather to compare the general nutritive value of each site. It is, therefore, significant to note that the general trends of effectiveness of the various treatments are the same on both sites. Phosphorus and potassium, combined as one application, increase the growth rate on both sites. Nitrogen alone also increases the growth rate to the extent of a combination of the two, this treatment being the most effective on both sites.

The experiments have shown that the general nutritive value of both substrates is probably fairly low, with available nitrogen, phosphorus, and potassium being present in sub-optimal amounts. However, the striking difference in growth rates of the control trees on the two sites must certainly indicate that the nutritional level of the coarse lean ore substrate is considerably lower than that of the stripping substrate.

In addition to these fertilizer experiments, pH tests were run on 5 representative samples of lean ore collected from various sites along the range. The values obtained ranged from pH 6.5 to 7.6 with an average of 7.0. Thus it is evident that the pH of the lean ore substrate is not an effective criterion in explaining the differences in observed growth rates, since the values obtained are comparable to those of the stripping till.

The comparison between growth rates of aspen on coarse lean ore and finely divided lean ore discussed earlier in this paper indicated a definitely better site quality of the latter. Some of this advantage may be due to a general higher level of substrate nutritive value, since this bank was the oldest lean ore site. However, it would seem more likely that the physical nature of the lean ore substrate is the limiting or controlling factor in the rate of vegetative growth on the lean ore banks. Where the lean ore is very coarse and resistant to weathering, hence low in colloidal particle content, growth is very slow. Conversely, where the lean ore is finely divided, the colloidal content may be relatively high and vegetative growth, therefore, more rapid.

An important distinction between the lean ore

and stripping spoil bank chronosequence was the striking difference in amount of herbaceous cover. In regard to the improvement in nutritive value of the two substrates with time, this difference becomes increasingly more important. The stripping bank succession was characterized by a very high incidence of nitrogen-fixing legumes, one of these, *Trifolium repens*, being prominent throughout the 51 yrs of spoil bank development. In contrast, the incidence of legumes in the lean ore succession was very low, *Trifolium repens* being almost entirely absent. In view of this fact, the nitrogen content of stripping spoil banks must certainly increase at a much faster rate than the lean ore banks. In addition, the much higher production of herbaceous vegetation in general on the stripping banks would account for greater amounts of organic matter being added to the soil with concomitant improvements in soil structure and increased nutrient supplies. While both substrates are undoubtedly low in available nutrients at the time of deposition and prior to extensive development of the pioneer vegetation, definite improvement in site quality can be expected on the stripping banks with the passage of time. On the other hand, the lean ore banks support only sparse and patchy vegetation, the coarse substrate particles are very resistant to weathering, and hence little improvement in site quality can be expected.

CLONE STUDIES

Since the most important woody species of the developing vegetation of both stripping and lean ore spoil banks are balsam poplar and aspen, a special study was conducted on the mechanism of vegetative propagation by which the seedling individuals once established expand their dominating influence over the landscape.

During the study on the vegetation chronosequence, clonal development of balsam poplar and aspen as a result of root suckering was evident on a number of the younger stripping spoil banks where the woody vegetation was sufficiently sparse to permit observation of this type of growth (Fig. 16). Probably the more densely wooded sites consist of series of fused clones, but it was impossible to distinguish

or isolate them under those conditions. The most favorable site for study was an extremely large stripping spoil bank deposited in 1925 and located 2 mi. northwest of Hibbing. Much of the uppermost surface was occupied by herbaceous vegetation with only isolated and widely separated clones of balsam poplar and aspen being present. As far as could be ascertained by visual inspection, most of the clones had apparently developed from one parent tree, since there was usually a distinct and gradual gradation in height from the tallest member near the center of the clone to the shortest members on the periphery.

The nature and occurrence of root suckers has been studied extensively in both balsam poplar and aspen (Brown 1935, Day 1944), and the same general conclusions apply to both species. Root suckers are produced by adventitious buds located on the surficial horizontal roots of the trees. According to Day (1944) and Zehngraff (1947), these buds remain dormant under shade and are activated only under strong sunlight. However, this cannot be completely true, since root suckers appear even under the dense canopies of various kinds of forest where aspen is present. Perhaps the activation of these buds may be somewhat inhibited, but certainly never completely prevented. The roots on which these buds are borne lie within 2 or 3 in. of the soil surface, and it has been shown by Clapham (1945) that light can penetrate a loose-textured soil to a depth of 3 to 5 in. Thus it is conceivable that light may have some influence on bud activation, but probably not to the extent reported by Day and Zehngraff.

Extremely rapid growth is attained by sucker shoots produced on well-developed root systems, some attaining a height of 3 or 4 ft in the first growing season. According to Day, root suckers may be produced as early as the second year's growth of a seedling. This was confirmed by observations made by the present author. Thus on the spoil banks in question, clonal development and expansion by the poplars is very rapid once seedlings have become established on the newly-formed surfaces, as will be seen from the observations described below.

METHODS AND PROCEDURES

A total of 7 balsam poplar clones was studied in the field to ascertain their morphology and rate of development. Profile sketches of each clone were drawn to show the gradation in height from the tallest tree to the periphery. A map view of each clone was drawn and the position of the tallest tree indicated. North-south and east-west transects were laid down bisecting the clone in each direction and the length of the clone along each axis recorded.

Each clone was studied to ascertain growth rates of the individual trees, the extent of clonal growth or enlargement along each axis, and soil profile characteristics. Along each transect line, the location of each tree within 3 ft of the transect line was plotted on the map view sketch. The height and



FIG. 16. General view of a typical balsam poplar clone.

basal diameter of each plotted tree were recorded, and basal sections or increment borings were obtained from each for age determination. Increment borings were also made of all of the tallest members of the clone to ascertain the age and location of the parent tree. In addition, a continuous shallow soil profile trench was dug along each transect line and measurements recorded of the thickness of the A_0 horizon and depth of the A horizon at 3 foot intervals along each axis.

RESULTS AND ANALYSIS

Since root suckers frequently have a greater growth rate than the parent tree, the tallest tree in the clone need not necessarily be the oldest. In order to avoid this variable, the location of the oldest tree in each of the 7 clones was ascertained by increment borings and the extent of expansion along the 4 cardinal compass headings from this tree were measured. In 5 of the 7 clones, the oldest tree was found to be the tallest also, while in the other 2, the oldest was somewhat shorter than adjacent individuals. In one clone, the distance from the tallest tree to the parent tree was 3 ft, while in the other the distance was 8 ft. The profile sketches of the 7 clones are presented in Figure 17 and show in almost every instance a pronounced greater extension of the clone in a southerly direction than in a northerly direction. This tendency was also observed in many other clones not studied in detail. While some variation in east-west expansion of the clones can be noted, there appears to be an average greater extension of the clone in an easterly direction also.

The results of the compass heading measurements confirmed the general impression imparted by the profile drawings. In each clone, southerly expansion from the parent tree was greater than northerly expansion, while expansion along the east-west axis was somewhat variable, though most pronounced in an easterly direction. The average southerly expansion was 33 ft (10.1 m) as compared to 21 ft (6.4 m) in a northerly direction, while the average expansion to the east was 28 ft (8.5 m) and to the west, 23 ft (7.0 m).

The greater expansion in a southerly direction of the clone is probably due to the influence of the shade cast by the clonal members. Not only would adventitious bud activation in the horizontal roots probably be inhibited on the shaded side, but soil temperature affected also. The southern half of the clone would receive direct insolation throughout the year. Hence the soil on the south should become frost-free earlier in spring and freeze later in the fall or winter than the soil under the shaded northern half. This would effectively lengthen the subterranean growing season on the southern edge of the clone and partially account for the more rapid expansion of the clone in that direction. During the earliest years of clonal development, the rate of expansion is probably nearly similar in all directions, since any shading effect would be non-existent. However, with continued

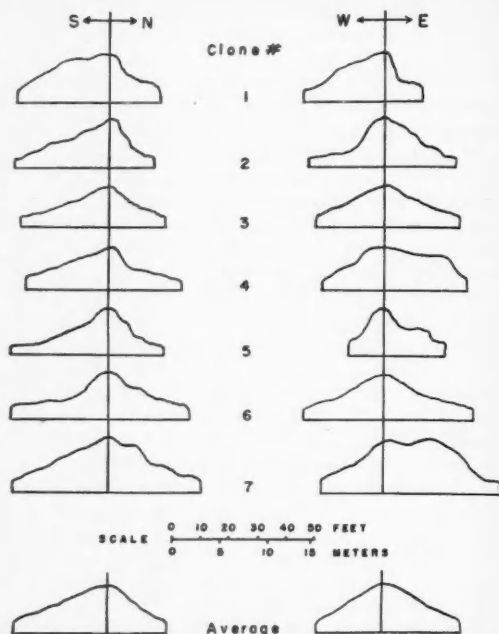


FIG. 17. Profile sketches of the 7 balsam poplar clones studied. Vertical axes represent position of oldest tree. Vertical scale same as horizontal.

vertical growth of the members of the clone, the rate of expansion on the northern side of the clone would be inversely related to the amount of shade cast by the members of the clone.

An attempt was made to ascertain the annual increase in clone area by year by comparing the age and distance from the parent tree for each tree recorded along the two transects of each clone. However, the data obtained by this method were extremely inconsistent, and no logical conclusion could be drawn from them. As Brown (1935) indicated, the production of sucker shoots by poplars is haphazard at best, both in time and distance from the parent tree. The sparsity of recorded trees along certain of the transect lines also made any calculation of annual rates difficult.

However, it was possible to obtain an overall rate of increase in clonal area. The average age of the parent tree in the 7 clones was 24 yrs, and the average distance to the periphery of the clone from the parent tree (average of all cardinal compass heading distances) was 26 ft. Thus the average rate of increase in clone radius for balsam poplar was 1.08 ft (33 cm) per year. This represents a rapidly increasing rate of areal expansion and suggests that only a small number of seedling establishments are needed on the spoil banks to produce a complete poplar cover within a given time. For example, seedlings could be established 50 ft apart in a hexagonal pattern, such as used in modern corn planting, on a new spoil bank and after only 25 yrs of development

could form a solid cover by root sucker production alone. Thus it is quite possible that the complete aspen canopy on the 32- and 51-yr old stripping banks is the result of fusion of individual clones rather than an initial abundance of seedling establishments. On the spoil bank of this clone study, the greatest distance between the clones was about 100 ft at the time of observation. If the rate of clonal expansion remains constant, a complete canopy of balsam poplar will be established in about 50 yrs without further seedling establishments.

In spite of the disparity in direction of clonal development, average growth rates of the individual tree stems were remarkably constant irrespective of their position in the clone (Table 11). One might

TABLE 11. Rates of height and basal diameter (BD) increase for balsam poplar on north, south, east, and west sides of clones.

Side of clone	Total number trees measured	Avg. height growth inches/year	Avg. BD increase inches/year
North.....	31	10.14	0.14
South.....	39	10.69	0.15
East.....	17	11.26	0.15
West.....	28	10.46	0.15

expect that the shading effect mentioned above would influence the growth rate of the trees as well as the extent of clonal development, since balsam poplar, like aspen, is one of the most intolerant woody species in the Lake States region. Yet those trees growing on the north side of the clones did not show significantly different growth rates from those in the other 3 sectors of the clone. The explanation for this uniformity in growth rate of the clonal members must lie in the fact that the members are connected with one another by the root system of the parent tree. In other words, a pathway is provided for interchange of growth materials from one tree stem to the next. Thus the trees on the southern side of the clone, while probably photosynthesizing at a greater rate than those on the shaded northern side, would share the products of this process with other members. Similarly water and mineral nutrients from the soil would be expected to be shared by the clonal members through this pathway.

No differences in soil profile characteristics were noted in the 7 clones, the average thickness of the A₀ horizon and depth of the A horizon being identical at the center and periphery in each clone. The average thickness of the A₀ horizon was 0.25 in. (0.64 cm) and the average depth of the A horizon 1.25 in. (3.18 cm). Apparently the amount of organic matter contributed by the herbaceous ground cover on the clonal periphery is approximately equal to that contributed by the clone or at least insufficiently different to create any noticeable differences in the profile at this stage. This would be consistent with the results obtained in the chronosequence study which showed no difference in soil horizon develop-

ment under herbaceous and woody cover on young spoil banks.

SUMMARY AND CONCLUSIONS

A study of the plant and soil chronosequence on Mesabi iron range stripping and lean ore spoil banks was conducted during 1952 and 1953. Plant and soil development over a period of 51 yrs was studied on the stripping spoil banks and plant development only for 31 yrs on the lean ore banks.

The stripping spoil bank succession usually led to a fairly uniform woodland community with *Populus tremuloides* and *P. balsamifera* being the conspicuous members of the overstory. Certain of the older stripping banks, however, had a predominantly grassland vegetation with only isolated clones of poplars being present. This may be due to poor seed crop years or to inadequate available moisture at the season when germination and establishment would normally occur in the 5 to 10 yr period following spoil bank deposition.

The herbaceous ground cover of the stripping bank woodland succession was dominated by *Poa pratensis*, *Trifolium repens*, and *Melilotus alba*. The first two are perennials and remain as conspicuous members of the ground cover throughout the succession, while *Melilotus alba*, a biennial, drops out within 30 yrs. The two perennials were also the important members of the grassland succession. *Phleum pratense* becomes one of the important members of the ground cover on the oldest banks.

Growth rates of aspen and balsam poplar were very low on all but the 51-year old stripping bank. The low organic matter and clay particle content, and high elevation above the ground water table are probably factors responsible for poor site quality on most of the stripping banks.

Soil profile development was quite constant through 21 yrs regardless of cover type, but dependent to some extent thereafter. The 41-year old bank had an A horizon depth of 2.5 in. under herbaceous cover, but only 1.75 in. under woody cover. A maximum thickness of the A₀ horizon (0.5 in.) was attained on the 51-year old bank.

Silt and clay content was very low on all sites sampled with the exception of the 51-year old bank. There was no evidence of B horizon development on any of the banks.

Some acidification of the upper soil layers was evident on the older banks. The 51-year old bank had a pH of 5.9 at a depth of 1 in. and 7.5 at 9 in.

Moisture equivalent values were closely correlated with clay content of the soil. Some increase was evident, however, on the 51-year old site which may be due to an increase in organic matter content of the surface soil layers.

Organic carbon content in the stripping bank soils increased from 0.08% at 2 yrs to 1.26% at 51 yrs at the 1 in. level. Total nitrogen increased from 0.005 to 0.098% at the same depth. Increases of less magnitude in content of both elements with

time were also evident at the 4 and 9 in. depths. The carbon-nitrogen ratio at the 1 in. depth decreased from a value of 18.0 on the 2-year old bank to 12.1 under herbaceous cover on the 41-year old bank and 12.9 under woody cover on the 51-year old bank. The continued high incidence of nitrogen-fixing legumes throughout the stripping bank succession was presumably the main reason for this pronounced decrease.

The lean ore bank succession was characterized by fairly abundant aspen and balsam poplar, the former attaining 100% frequency on the oldest bank. The herbaceous ground cover was very sparse throughout the 31 yrs of development. The lean ore substrate is probably quite suitable for aspen and balsam poplar seed germination because of the numerous micro-habitats provided by the coarse-textured surface and the lack of competition by a ground cover vegetation.

Growth rates of aspen and balsam poplar on young, coarse-textured lean ore banks were extremely low, much less than growth rates on stripping banks of comparable age. In addition, the trees were usually deformed and very susceptible to insect and fungal attacks. However on the 31-year old site, growth rates were much better and the trees less deformed. The lean ore of this bank was finely divided in contrast to the others. It is suspected that this is the major factor in producing better growth rates rather than improvement in nutritive values of the substrate with time.

Fertilizer experiments were conducted on young coarse lean ore and stripping banks, using aspen as the test species, to ascertain possible differences in nutritive value between the two substrates. Available nitrogen, phosphorus, and potassium were present in sub-optimal amounts in both substrates and the general nutritive value of both was low. Hence the better growth rates attained by aspen on the young stripping banks was probably due to the more favorable texture and higher colloidal particle content of the stripping material. Reasonable improvement in site quality of the stripping banks can be expected with time because of the abundance of herbaceous vegetation, especially nitrogen-fixing legumes. Only slight improvement in site quality can be expected on the lean ore banks because of the sparseness of herbaceous cover, especially legume species, and the resistance of the lean ore particles to weathering.

Clonal development of aspen and balsam poplar was observed on a number of the younger stripping spoil banks as a result of root suckering, and a study was made on 7 balsam poplar clones to determine their morphology and rate of development. A pronounced greater extension in a southerly direction of practically all clones was evident which is probably due to greater bud activation on the surficial roots, higher soil temperature, and a longer subterranean growing season on the southern edge of the clone. The average rate of radial expansion of clones was slightly more than 1 ft per year for 22- to 26-year

old clones, indicating that only a small amount of initial seed reproduction is necessary on a newly deposited bank eventually to produce a complete canopy of aspen and balsam poplar. Growth rates for the individual trees of the clones were remarkably constant in spite of the differences in direction of expansion and amount of shade. Interchange of growth materials through the interconnecting root system of the clone members probably accounted for the uniformity in growth rates.

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THE DOUGLAS-FIR ZONE OF SOUTHERN INTERIOR BRITISH COLUMBIA

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INTRODUCTION

One of the most extensive and characteristic plant vegetational zones of interior British Columbia is that dominated by Douglas-fir. This zone occurs in the southern interior region of the Province, between the higher elevations of the Rocky Mountain system on the east and the Coast Range on the west. Its northern limit lies just beyond Lat. 53°, while southward it is continuous with the main body of the Rocky Mountain Douglas-fir forest.

Pseudotsuga menziesii (Douglas-fir) is the principal climax tree of the zone, and forms almost pure stands in areas relatively free from disturbance. The form of Douglas-fir found in this region differs from the typical coastal tree in size, growth form, and drought resistance, and has been referred to the variety *glauca*. Due to various disturbing factors, particularly fire, large portions of the zone are currently dominated by other tree species. The most important of these are *Pinus contorta* (lodgepole pine), *Populus tremuloides* (aspen), *Pinus ponderosa* (ponderosa pine) and species of *Salix*.

Few ecological studies have been made of the native vegetation of interior British Columbia. The general zonal pattern of vegetation and soils has been described (Spilsbury & Tisdale 1944), but investigations of the forested areas have dealt mainly with the commercial timber resources. The Douglas-fir zone is of particular interest, constituting as it does the northern extremity of one of the principal forest communities of North America. Many influences including fire, insects, logging and grazing have affected the vegetation, producing highly significant changes.

Due to its extent and multiple land values, this zone is one of major importance in British Columbia. Successful management of such lands depends on an understanding of the interrelationships of climate, physiography, soils, vegetation and animal life within the zone. The present study is offered as a contribution to this understanding and as background for other research now in progress.

The studies discussed in this paper were made principally during the years 1935 to 1940 and in 1946 and 1947. During the former period the senior author, as a member of the staff of the Dominion Range Experimental Substation at Kamloops, initiated much of this research. Following the closing of the Substation in 1941, work was confined to annual inspection trips until the summer of 1946 when intensive studies were resumed and continued in 1947. Since that time certain critical points have been checked and some additional data collected.

The authors are indebted to many persons for advice and help in this study. Dr. W. S. Cooper, Botany Department, University of Minnesota, gave constant encouragement and helpful criticism. Many persons, including J. D. Elliot, D. K. Taylor, T. G. Willis and others, aided at various times in the field studies.

Identification of the vascular plants was checked by Dr. H. A. Senn and staff of the Division of Botany, Science Service, Ottawa; the mosses were determined by Dr. Frances Wynne, New York Botanical Garden and Dr. H. S. Conard, Grinnell College. Dr. Grace Howard, Wellesley College, and Dr. J. W. Thompson, University of Wisconsin, named the lichens.

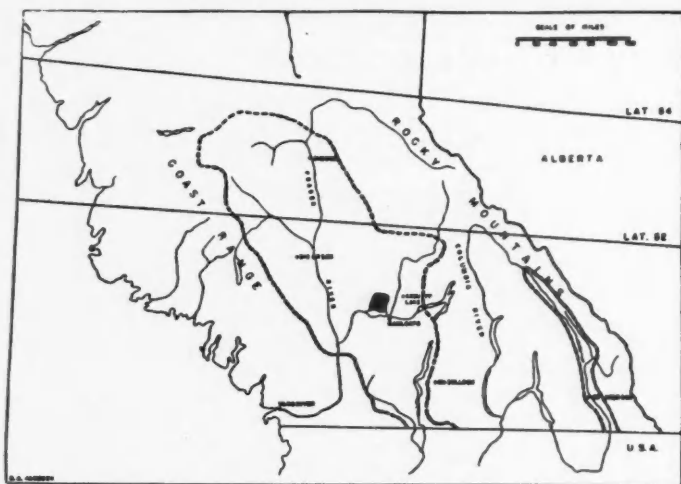


FIG. 1. Outline map of southern British Columbia showing approximate outer limits of Interior Pseudotsuga zone (inside broken lines) and location of Tranquille Forest (shaded area).

DESCRIPTION OF THE AREA

LOCATION AND EXTENT

The approximate extent of the Douglas-fir zone of interior British Columbia is indicated in Fig. 1. This map has been compiled from a variety of sources, including publications by Halliday (1937), Whitford & Craig (1918) and observations by the writers. The zone occupies an area about 375 mi. long from north to south and contains approximately 15 million acres. By way of comparison, the grasslands of the same general region cover about 3 million acres.

Over much of the southern portion of the region, contact with other vegetation zones is relatively sharp. Toward the northern portion the limits of the Douglas-fir community are not so well-defined. A gradual transition to *Picea/Abies* forest occurs in the area north of Quesnel. A lesser ecotone occurs on the southeastern side where contact is made with *Thuja/Tsuga* forest. Here Douglas-fir mingles with the dominants of the latter community, especially with *Thuja plicata*.

While studies were made in various parts of the region, the bulk of the detailed work was done on the Tranquille Provincial Forest. This forest, situated northwest of the city of Kamloops (Fig. 1), contains about 260 sq mi, with about one-half of the area in the Douglas-fir zone. The climate, soils and native vegetation of the area are typical of much of the southern interior of the Province.

GEOLOGY AND PHYSIOGRAPHY

The bed rock includes deposits of Cenozoic, Mesozoic and Paleozoic age, but Tertiary deposits are of major importance over most of the area. Prior to the uplift and subsequent erosion of the late Tertiary

period, the lava plains of the region are thought to have been continuous with the Columbia lavas of Washington, Oregon and Idaho (Brock & Schofield 1933).

During the Pleistocene the whole region was glaciated by the Cordilleran ice sheet which advanced from the north. This glaciation left a marked impression on the topography, rounding off hills and ridges, and widening and straightening pre-glacial valleys.

The retreat of the ice sheet left a mantle of glacial till over the region. In places this cover was thin and easily removed by subsequent erosion, with the result that rock outcrops are common at the present time. Over most of the area the till remained, and has formed the parent material of most of the soils of the region.

Physiographically, the study area constitutes part of the interior Plateau System (Brink & Farstad 1949). This region is characterized by a series of irregular plateaus, separated by broad, deep valleys and contains several small mountain ranges. The northern portion is the least rugged, and contains considerable areas of undulating to rolling land.

The numerous valleys constitute one of the most conspicuous features of the region. The larger ones are wide and U-shaped with well-marked terraces. The valley floors are from 2,000 to 4,500 ft below the level of the surrounding uplands. Drainage is mainly to the west by way of the Fraser River and its tributaries, which include the Thompson and the Chilcotin Rivers. In the southeastern portion there is some drainage south through the Columbia and its tributaries.

The general plateau level slopes upward from north to south. The average elevation of the northern

portion is about 2800 ft above sea level, as compared to 5000 ft at the southern border.

The Tranquille Forest and adjacent lands constitute a typical section of the whole region, both geologically and topographically. A series of rugged slopes beginning at an elevation of 1100 ft in the Thompson River Valley reach the height of land at 6000 ft on Poreupine Ridge, about 20 mi. to the north. Below the 5000 ft contour the topography is hilly, while above that level the plateau character is more evident. The area is drained by the Tranquille River which flows into the Thompson.

CLIMATE

The climate of the area is conditioned by the presence of a mountain barrier to the west, and by local topography. Air currents moving eastward from the Pacific are cooled and lose most of their moisture in passing over the Coast Range. Once over the summit, they are warmed again and remain relatively dry until the next major range (the Columbian System) is reached. Here again precipitation is abundant on the west slopes and scanty on the eastern slopes. Thus there are produced two Dry Belts, the more westerly and larger of which includes the greater part of the interior Douglas-fir zone (Fig. 1).

Locally, climate is affected greatly by topographic differences. Elevation is a major factor, producing vertical zonation of climate, soils and vegetation (Spilsbury & Tisdale 1944). Exposure is important also in an area of such rugged topography. The elevational boundaries of the main vegetation zones on south and west slopes differ by about 800 ft from their equivalents on north and east exposures.

Variations in climate within the region are not well shown by the records of the regular meteorological stations, most of which are located in the principal valleys, where settlement is concentrated. Data for a few representative localities, together with the type of native vegetation occurring in the immediate vicinity, are presented in Table 1.

The data show something of the climatic differences encountered in passing from one of the drier portions of the grasslands (Kamloops) through to the spruce/fir zone (McCulloch). The data are not nearly so satisfactory as would be those from a series of field stations located in representative portions of each of the zones, but such information is not available at present. In a general way, these data indicate that the *Pseudotsuga* zone is moister and cooler than the grasslands or *Pinus ponderosa* and drier and warmer (in summer at least) than the *Picea/Abies* zone. Critical data for zonal ecotones are lacking.

The data for the Douglas-fir zone do not include a station located in the major study area on the Tranquille Forest. Knouff Lake represents the closest approximation, but is located close to the upper limits of the zone, and the short-term record indicates unusually low winter temperatures. Of the two more northerly stations in the zone, Big Creek is notable for low annual precipitation. Apparently

effective precipitation at this station is increased by low temperatures brought about by a combination of elevation and latitude.

Fragmentary climatic records not shown in Table 1 have been obtained with standard weather instruments at the Pass Lake field station, located at an elevation of 3150 ft, near the lower margin of the Douglas-fir zone in the Tranquille Forest. No year-long precipitation data are available, but the mean for the period April through September in 4 yrs (1939, 1940, 1949, 1950) was 6.41 in. The corresponding figure for Knouff Lake is 8.35 in., and for Kamloops 4.5 in. The mean July temperature for a 6 year record was 60° F, slightly higher than at Knouff Lake.

The seasonal distribution of precipitation in the Douglas-fir zone is similar to that occurring in the grasslands (Tisdale 1947) and apparently over the region generally. There are two annual maxima, one in May and June, the other in December and January. March and April are the months of minimum precipitation. The percentage of the annual precipitation occurring during the April-September period averages 52 for all sites in Table 1 and 54.5 for the 3 sites in the Douglas-fir zone.

Most of the rainfall comes in relatively gentle storms, and runoff is slight except on extremely steep or unprotected slopes. There is a permanent winter snow cover in the Douglas-fir zone amounting, in the Tranquille Forest, to about 2 ft and lasting usually from late October until late April.

In a study where plant succession is involved, it is important to know whether climatic conditions deviated greatly from normal during the period under consideration. Comparison of data for the period 1935-1947 with the long-term averages indicates that precipitation and temperatures did not depart significantly from the normal. At Kamloops, for example, the mean precipitation for the April to September period was 5.8 in. during this period, compared to 5.6 in. for the 59-yr average.

In 1936, 1941, and 1942, conditions for plant growth were noticeably above average, while relatively poor growing seasons occurred in 1937, 1938, 1940, and 1943. There was no prolonged period of years during which climatic conditions were significantly more or less favorable than average.

SOILS

Soil studies in interior British Columbia have been relatively few to date, with attention concentrated mainly on areas of value for cultivation. R. H. Spilsbury & Tisdale (1944) have provided some data for the Douglas-fir and associated zones.

The soils of the region are derived mainly from glacial till, much of which has been sorted by water (Kelley 1940). A wide range of textures occur, with sandy loams most common. In many areas a high percentage of parent rock fragments is present in the profile.

TABLE 1. Climatic data for representative stations in southern interior British Columbia.¹

Station	Latitude (degrees)	Elevation (feet)	Vegetation zone	MEAN PRECIPITATION		MEAN TEMPERATURES	
				Annual (inches)	Apr. - Sept. (inches)	Jan. (degree F.)	July (degree F.)
Kamloops.....	51	1133	Agropyron/Poa	10.2	5.58	22	70
Hedley.....	49	1700	Pinus ponderosa	11.52	5.72	22	68
Knouff Lake.....	51	3750	Pseudotsuga	15.43	8.05	8	57
Big Creek.....	52	3100	Pseudotsuga	12.32	7.33	13	58
Quesnel.....	53	1750	Pseudotsuga	16.43	8.75	15	62
McCulloch.....	50	4100	Picea/Abies	26.99	11.9	15	56

¹Records are for periods of 25 years or more, through 1954, except the temperature records for Knouff Lake (6 years) and McCulloch (15 years).

Several major soil zones are represented, each associated with a distinct plant community in the pattern of zonation characteristic of the region. The grassland soils include the Brown, Chestnut and Black (Chernozem) groups. The forest areas have not been fully classified, but work done to date indicates the occurrence of at least two types of podsolie soils associated with the Douglas-fir and spruce/fir zones respectively. Recently Beaton (1953) has classed as Brown Podsolie soils from the upper portion of the Douglas-fir zone near Kamloops.

A typical profile for the Douglas-fir zone in the Tranquille area has been described as follows (Spilsbury & Tisdale 1944):

Horizon	Depth	
A ₀	1½"	Dark brown organic mat, partially decomposed and fibrous.
A ₂	0-2½"	Ash grey loam, gritty, structureless and porous.
B ₁	2½"-10"	Light yellow brown (creamy colored) loam, amorphous and slightly dense.
B ₂	10-25"	Drab brown clay loam, dense, tough, large angular nut structure.
C	25"	Grey brown loam, unweathered, strongly cemented glacial till; the top inch may contain free lime streaks.

An ash-grey leached layer forms the A₂ horizon, while the B₁ has a light brown or creamy color. There is a considerable accumulation of clay in the B₂ horizon. The chemical composition of this type profile is summarized in Table 2.

The humus of this profile type has a relatively high base status and high pH for a podsolie soil. This is related to the presence of a well-developed herbaceous cover, high in bases. Organic matter shows a marked decrease with depth, indicating a stable colloid form which has not been eluviated to any extent. Leaching of iron and aluminum from the A horizon has occurred, but not to a marked degree.

The profile type in the spruce/fir zone shows stronger leaching of the upper horizons, more accumulation of clay and organic matter in the B horizons and

TABLE 2. Chemical composition of typical soil profile in the Douglas-fir zone, Tranquille Forest.

Horizon	Depth in.	SiO ₂ %	Fe ₂ O ₃ %	Al ₂ O ₃ %	CaO%	MgO%	Organic Matter%	N%	pH
A ₀	1½	48.2	5.2	8.3	2.6	3.1	20.6	0.46	5.8
A ₂	0-2½	63.7	6.0	13.3	2.7	2.8	2.8	0.09	6.5
B ₁	2½-8	60.1	7.6	15.0	2.9	2.2	1.7	0.08	6.2
B ₂	8-23	52.9	12.2	16.0	3.6	4.1	0.88	0.04	7.1
C	23	54.0	11.3	15.9	4.4	5.3	0.42	0.03	7.0

greater acidity (pH 5.5 in the A₂ horizon).

The texture of the soils examined in various associations of the Douglas-fir zone varied from gravelly loams to clay loams, with loams most common. No large areas of coarse-textured soils were studied, although some occur in the central and northern portions of the zone. The relatively fine texture and considerable depth of most soils in the zone may seem surprising in view of the rugged and rocky nature of the region. The reason evidently lies in the presence of a mantle of glacial till over most of the area.

REVIEW OF LITERATURE

The zonation of forest vegetation in western North America has been the subject of many investigations, beginning with the classical study of the San Francisco Mountain region by Merriam (1890). Pearson (1931) recognized 7 altitudinal zones in Arizona, these including a Douglas-fir community situated between the ponderosa pine and the spruce/fir. The Douglas-fir type is described as containing considerable ponderosa pine in the lower portion of the zone and *Picea engelmannii* in the upper part.

Daubenmire (1943, 1946) describes 6 major vegetational zones in the Rocky Mountain region. Two of these, *Pinus ponderosa* and the *Pseudotsuga*, represent subdivisions of the "Montane zone" of Weaver & Clements (1938). The Douglas-fir zone, as described by Daubenmire, has this species always well represented in the climax, with *Picea engelmannii* and *Abies lasiocarpa* lacking. Ponderosa and lodgepole pine, as well as aspen are recognized as important seral species, especially on burned areas. In a later paper Daubenmire (1952) recognizes two associations, the *Pseudotsuga/Physocarpus* and *Pseudotsuga/*

Calamagrostis, within the Douglas-fir zone in northern Idaho and adjacent Washington. Only the first of these associations is described in any detail by Daubenmire, as the second is poorly represented in the area studied by him.

Six vegetational types associated with a similar number of zonal soil groups were recognized by Spilsbury & Tisdale (1944) in the southern interior of British Columbia. The "Montane zone" of that study corresponds to the Douglas-fir zone described in the present paper. Tisdale (1950) reported briefly on grazing values and successional stages caused by fire in this zone.

Kujala (1945), a Finnish forester, described a number of forest types during a 3-month visit to British Columbia in 1931. These communities were classified purely on the basis of the undercover vegetation, without regard to successional status. Kujala's "*Arctostaphylos-Calamagrostis* type" and possibly his "*Calamagrostis* type" appear to correspond to two of the communities described in the present paper. Nine of the 10 sites in Kujala's "*Arctostaphylos-Calamagrostis* type" were dominated by seral tree species, mainly *Pinus contorta*, while *Pseudotsuga menziesii* was dominant on one site.

Earlier observations on the Douglas-fir zone of interior British Columbia are relatively few and occur scattered among reports dealing primarily with the geology and general plant life of the region. Macoun (1876) describes the Douglas-fir forest occurring directly above grassland in the Lytton region with the lower forest boundary at an elevation of 3400 ft above sea level (the same as it is today). Farther north in the region Macoun found that "the original forest of Douglas-fir had been burned and had been commonly replaced by poplar (aspen), *Pinus contorta*, birch and willows." Dawson (1894) in his report on the geology and natural features of the Kamloops area refers to the abundance of lodgepole pine in areas obviously belonging in the Douglas-fir zone, and remarks on the abundance of fires caused by both whites and Indians.

Whitford & Crain (1918), in their report on the forests of British Columbia recognized several major communities in the "Dry Interior," including the "yellow pine type and interior Douglas-fir type."

The report on the forest resources of the Province by Mulholland (1937) treats forest types primarily from the viewpoint of timber production. The effects of fire and insects are stressed, annual losses from these sources being greater than the amount taken yearly by logging at the time this report was issued.

The most complete classification of forest types in British Columbia is that made by Halliday (1937) who divided the "Montane forest" of interior British Columbia into four sections as follows: 1—Yellow pine and Douglas-fir; 2—Central Douglas-fir; 3—Northern aspen; 4—Montane transition. Section 1, the most southerly and xeric, is further divided into two associations, one dominated by ponderosa pine, the other by Douglas-fir. Whether the latter is really

different from the "Central Douglas-fir type" is open to question. Halliday's forest "sections" are based largely on existing composition rather than on climax vegetation. Section 3 is described as dominated by aspen along with lodgepole pine, Englemann spruce and scattered Douglas-fir. This may be a Douglas-fir climax altered by fire, but the abundance of Englemann spruce is not a feature to be expected. The "Montane transition" is described as having Englemann spruce and alpine fir as its "characteristic and most widely distributed association," while "scattered through is Douglas-fir which would appear to have had formerly a greater representation." The abundance of spruce and alpine fir together with other characteristics of the "section" indicate that it belongs to the spruce/fir rather than to the Douglas-fir zone. It is possible that *Pseudotsuga* was formerly dominant, and is being replaced by *Picea* and *Abies* in the shift towards more mesic vegetation which seems to be occurring at present in central and north-central British Columbia (Brink & Farstad 1949).

The effects of fire on the Douglas-fir and adjacent forest zones have been the subject of considerable investigation. Clements (1910) showed that in Colorado stands of lodgepole pine and aspen developed in the Douglas-fir and spruce/fir zones as a result of repeated fires. Fire produced conditions well suited for the reproduction of lodgepole pine, which is an excellent seed producer but has hard cones and is unable to reproduce in stands of the climax dominants. The forest zones described by Clements in northern Colorado resemble to a striking degree those found in interior British Columbia.

The role of aspen in relation to fire has been established by many studies, including those of Baker (1925) and Moss (1932). It has been shown that aspen reproduction after fires takes place chiefly by means of adventitious shoots arising from the roots. Reproduction by seed appears to be less common, due apparently to the short period of viability for aspen seed and its slow initial root growth (Moss 1938) as well as to frequent lack of seed trees following fires. Aspen seedlings were observed in considerable numbers, however, by the authors on several burned areas in the Douglas-fir zone of the Kamloops region in 1952.

HISTORY OF PAST USE

The recent history of the Douglas-fir zone in interior British Columbia is one in which fire, insects, lumbering, and grazing have all been important. Early historical records and studies of past burns indicate that fire has long been common in this zone. Fires caused by lightning occur at the present time and presumably were a factor in the past. Records of the Kamloops Forestry District, which includes large areas of the Douglas-fir zone indicate that lightning caused from 15 to 43% of all forest fires during the period 1952 through 1955. Man-made fires probably have been a normal occurrence for a long time, for there is evidence that the native

Indians were accustomed to setting fires in both grassland and forest areas in order to make better hunting grounds (Guichon 1953). The incidence of fires evidently was increased temporarily with the coming of the white man, particularly during the period 1870 to 1890, when railroad construction and prospecting were most active. The importance of fire as a disturbing agent in recent times is indicated by data for the Tranquille Provincial Forest reported by the B. C. Forest Service (1931). During the period 1850-1931 there were 22 known fires which burned 57% of the area. Approximately two-thirds of the fire damage was done during the period 1870-1890. The incidence and size of fires has declined during the past few decades with further settlement of the country and the development of better fire control facilities.

Of the insects inhabiting the Douglas-fir zone, perhaps the most destructive in recent decades have been bark beetles, species of *Dendroctonus* and *Ips*. These insects were particularly active in the southern interior of the Province from 1927 to 1937, during which time they killed as much as 60 to 95% of the trees in many stands of lodgepole pine. The effect of these insect attacks was to create numerous and often extensive "deadfall" tracts in the large areas occupied by the pine.

Logging has been carried on in interior British Columbia since the 1860's, but until recently only ponderosa pine had been severely affected. More recently Douglas-fir has come to be logged on a large scale. Lodgepole pine and aspen are still almost untouched in the region due to the abundance of the above mentioned more desirable species.

Grazing by livestock was a relatively minor influence until recently. Ranching began in the 1860's, but during the first few decades was confined largely to the grasslands and the ponderosa pine zone. Depletion of the grasslands together with increasing numbers of livestock forced stockmen to make greater use of forest areas for summer grazing. At present the majority of the cattle in the region are grazed on forest ranges during the summer season (June 15 to September 30 approximately). It is estimated that about 8 million acres of forest are now used for grazing in the interior (British Columbia Forest Service 1952) and of this area, probably two-thirds lies in the Douglas-fir zone. On lands of this type, where fire is controlled, grazing is frequently the major influence exerted by man.

The Douglas-fir zone in the Tranquille Forest remained almost unaffected by livestock grazing prior to 1935. In that year, summer grazing of a portion of the area was begun and has been continued since that time.

METHODS OF STUDY

The plant species of the zone were collected and identified over a period of years. A complete collection has been deposited in the herbarium of the Range Experimental Farm at Kamloops. Specimens

of the principal species were also placed in the herbaria of the Division of Botany, Science Service, Ottawa and the Range Management Herbarium, University of Idaho.

In the earlier stages of the study, a reconnaissance of several areas in the Douglas-fir zone was followed by the more detailed study of a number of representative stands scattered throughout the zone. On temporary plots approximately 100 sq. m in area site features such as elevation, slope and exposure were described. The vascular plants and more conspicuous mosses and lichens were listed and their abundance rated on a 5 figure scale (Braun-Blanquet 1932). In addition, the dominant species of various vegetational strata were indicated. One or more soil pits were dug, the profile described and samples taken for mechanical and chemical analysis.

For the more intensive community studies, series of sample plots, most of them 5 x 20 m in size, were established in 1946 through 1948. The whole plot was used for study of the trees and larger shrubs while the smaller shrubby species were studied on a sub-plot measuring 1 x 10 m. The frequency of all species rooted within the study plot was recorded on 25 plots 0.2 by 0.5 m in size. These frequency plots were used primarily as a rapid means of evaluating the herbage and moss-lichen cover. Preliminary tests indicated a close correlation between frequency of the principal species of these strata on this size of plot and their abundance as determined from quadrats 0.5 and 1 sq m in area. Yields and height measurements of herbs and shrubs were taken in quadruplicate on plots measuring 0.5 x 1 m. All herbage was clipped to ground level and the current year's growth of shrubs was taken. The clippings were divided into 5 classes based on life-form and palatability to cattle. The frequency plots were established systematically along one side of each major sample area, while the yield plots were located systematically along the center line.

The large sample plots were located at random on sites selected as representative of the principal plant communities recognized in the zone. Selection was made on the basis of previous study and a thorough inspection of many areas. In most cases, two or more major sample plots per site were established. The 100 sq m size proved large enough to include 20 to 30 trees per plot in most stands and provided ample space for the smaller plots used for shrubby and herbaceous species. In mature Douglas-fir stands, the plot size was increased to 250 sq m in order to include a tree population per plot approximating that obtained on 100 m in stands of *Pinus*, *Populus* and immature *Pseudotsuga*.

PRINCIPAL COMMUNITIES OF THE PSEUDOTSUGA ZONE

Certain studies of the Douglas-fir zone including investigations of habitat factors and phenology of the principal species were started by the senior author as early as 1935. The first effort to analyze the

plant communities was made in 1938 and 1939 when 35 temporary sample plots were established in the zone as part of a broad study of soil-plant relationships and zonation (Spilsbury & Tisdale 1944). The results of this study revealed the presence of two major seral communities dominated by *Pinus contorta* and *Populus tremuloides* respectively in the Tranquille area. The data also indicated differences in the nature and amount of the shrubby and herbaceous vegetation associated with each of these communities.

Observations made during the course of study from 1935 to 1939 and subsequently at numerous locations in the southern interior indicated the presence of vegetation similar to that found on the Tranquille area. This fact, together with the need for data of a more detailed and quantitative nature led to further work during the period 1946 to 1948.

In 1946 methods for the detailed study of the various strata were worked out, and a number of study areas selected. In 1947 and 1948, sample plots were established on 9 representative sites in the Tranquille Forest.

Certain results from these studies are summarized in Fig. 2 and Tables 3, 4 and 5.

These data serve to show some of the features of the composition of each community, and some of the differences existing among them. Further details are presented in the discussion of each association.

CONCEPTS AND TERMINOLOGY

Due to differences in the interpretation and use of certain ecological terms, some consideration of the concepts followed in this paper regarding classification of vegetation appears to be warranted. Vegetation is considered climax or permanent if it appears to be self-regenerating and there is no concrete evidence that it is followed by a different community. Seral vegetation is indicated by the temporary status of at least some of its species and by a demonstrated tendency for changes to occur through normal succession.

The basic unit in vegetation classification is considered to be the association, which is formed by a distinctive combination of vegetational strata or unions. The association concept is based on the existence of actual stands which, despite considerable variation, bear a closer resemblance to one another than to stands of other associations. The term association is used for climax vegetation, while equivalent units of seral vegetation are termed associes.

Plant community is used as a general term to indicate an organized grouping of plants, with no implication as to the size or permanence of these groupings. Vegetational zone is used to indicate a climax community of major status composed of one or more associations. The term is used to indicate the whole area which either supports such vegetation now or could be expected to support it by the natural replacement of existing seral vegetation. Thus one may designate a *Populus/Calamagrostis* associes of the *Pseudotsuga* zone where the evidence indicates that

Populus is a seral dominant in an area where *Pseudotsuga* is the principal tree in the climax vegetation.

For more detail on viewpoints similar to those

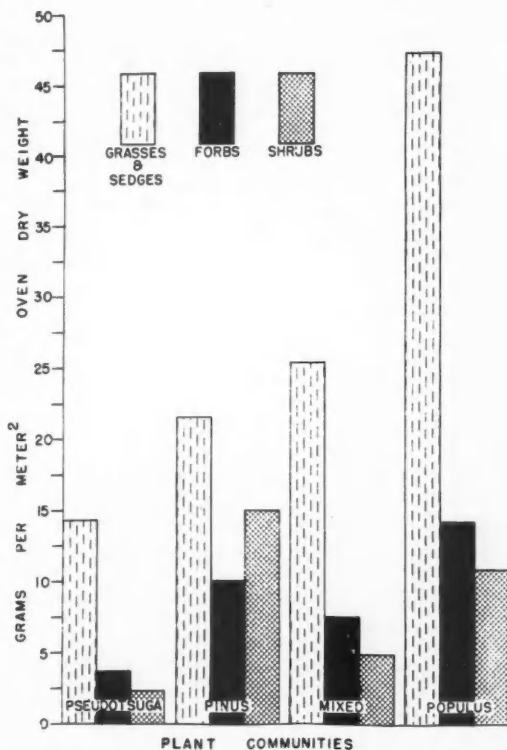


FIG. 2. Comparison of yield of different classes of undercover vegetation in 3 plant communities and one mixed stand in the *Pseudotsuga* zone of the Tranquille Forest, 1947. For brevity, each community is named according to its dominant tree species only.

TABLE 3. Average basal area of tree species in different communities in the Douglas-fir zone, Tranquille Forest.

Species	BASAL AREA IN SQUARE FEET PER ACRE ¹			
	Plant Community			
	Pseudo-tsuga	Pinus contorta	Populus	Mixed Conifer-Populus
<i>Pseudotsuga menziesii</i> var. <i>glauca</i> (Beissn)				
France	205.97	43.23
<i>Pinus contorta</i> Dougl.	3.47	144.82	0.11	53.54
<i>Populus tremuloides</i> Michx.	3.08	90.05	23.32
<i>Pinus ponderosa</i> Laws.	0.87
<i>Salix</i> spp.	17.70	0.70
Total	227.14	147.90	90.16	121.66

¹Average for all study sites in each community.

TABLE 4. Density of shrubs in different communities in the Douglas-fir zone, Tranquille Forest.

Species	AVERAGE NUMBER OF PLANTS PER 100 SQUARE METERS							
	Plant Community							
	Pseudotsuga		Pinus contorta			Mixed Conifer-Populus	Populus	
	Site 1	Site 3	Site 1	Site 2	Site 3		Site 1	Site 2
<i>Amelanchier alnifolia</i> Nutt.	4	2	1.5	1	...	18	14	2
<i>Juniperus communis</i> L.	0.5	1
<i>Shepherdia canadensis</i> (L.) Nutt.	3	16	3	6	6	4	2.5	10
<i>Rosa gymnocarpa</i> Nutt.	90	110	115	90	80	440	150	240
<i>Spiraea betulifolia</i> Pall.	40	35	170	120	120	310	65	100
<i>Symphoricarpos albus</i> (L.) Blake	(1)	3

(1) Dense patch in 1 corner of plot, number of stems not counted.

TABLE 5. Percentage frequency of principal species in the herbaceous and moss-lichen strata of different communities in the Pseudotsuga zone, Tranquille Forest.¹

Species	PLANT COMMUNITY			
	Pseudo- tsuga	Pinus contorta	Conifer- Populus	Populus
Herbaceous-Dwarf shrub stratum				
<i>Achillea lanulosa</i> Nutt.	5	..	9	24
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	24	34	16	14
<i>Arnica cordifolia</i> Hook.	28	26	31	28
<i>Astragalus serotinus</i> A. Gray	6	..	20	10
<i>Aster conspicuus</i> Lindl.	15	10	15	28
<i>Berberis repens</i> Lindl.	3	9	25	45
<i>Calamagrostis rubescens</i> Buckl.	100	100	100	100
<i>Carex richardsonii</i> R. Br.	23	27	14	13
<i>Fragaria glauca</i> S. Wats.	42	26	50	27
<i>Galium boreale</i> L.	..	1	9	18
<i>Goodyera oblongifolia</i> Raf.	14	10	..	3
<i>Hieracium albiflorum</i> Hook.	13	8
<i>Hieracium umbellatum</i> L.	2	5	17	12
<i>Lathyrus ochroleucus</i> Hook.	48	26	48	87
<i>Linnaea borealis</i> L.	36	85	8	5
<i>Lupinus glacialis</i> C. P. Smith	..	74	..	40
<i>Pyrola secunda</i> L., <i>P. asarifolia</i> Michx.	15	15	2	2
<i>Taraxacum officinale</i> Weber	6	..	2	15
<i>Thalictrum occidentale</i> A. Gray	15
<i>Vaccinium caespitosum</i> Michx.	5	54	2	..
<i>Vicia americana</i> Muhl.	5	5	22	34
<i>Viola adunca</i> J. E. Smith	5	3	26	14
Moss-Lichen Stratum				
<i>Brachythecium</i> spp.	17	10	3	2
<i>Peltigera aphthosa</i> L., <i>P. aphthosa</i> (L.) Willd.	30	9	4	..

¹Only species with frequency values of 10% or more in at least one community are included. Frequency was calculated as:

$$\frac{\text{No. of quadrats in which a species occurs}}{\text{Total no. of quadrats examined}} \times 100.$$

summarized here, the reader is referred to the excellent discussion by Daubenmire (1952).

THE PSEUDOTSUGA/CALAMAGROSTIS ASSOCIATION

Representative study areas in this community were not easy to find, due to the effects of past fires, and to heavy grazing use of certain areas. Site 1 appeared to represent the more xeric portion of the zone, while Site 2 was more mesic. The former site is located on a south slope of about 10% at an elevation of 3300 ft. The soil mantle consists of 10

TABLE 6. Data for tree stands on 2 sites in the *Pseudotsuga/Calamagrostis* association of the Pseudotsuga zone, Tranquille Forest.

Species	Site	No. INDIVIDUALS		Average Tree Height (Feet)	Average Tree Age (Years)	Average d. b. h. (Inches)
		(Per 250 M ²) Trees	Reprod.			
<i>Pseudotsuga menziesii</i>	1	9.5	40	67	175	13.6
	2	13.0	43	65	220	12.6
<i>Pinus contorta</i>	1	59	..
	2	5	..	50	..	4.6
<i>Pinus ponderosa</i>	1	1	0.5	80	210	17.0
	2
<i>Populus tremuloides</i>	1	..	2.0
	2
<i>Salix</i> spp.	1
	2	2	4	20	..	2.3

in. of clay loam overlying sandy loam. The profile contains numerous rock fragments. Site 2 is situated at a slightly lower elevation, on a virtually level area. The soil is slightly finer in texture and less stony than at Site 1. Two sample plots were established at Site 1 and 1 plot at Site 2. Data for the tree cover on the 2 sites are presented in Table 6.

It is evident that the tree cover of both sites consisted of a relatively open stand of nearly mature *Pseudotsuga* along with a sprinkling of other species (Figs. 3, 4). *Pinus ponderosa* was confined to one plot at Site 1. Mature specimens of this species occurred on south slopes to elevations of 3900 ft in this vicinity, well above the normal elevational range. *Pinus contorta* was found only at Site 2, where its presence appeared due to a fire occurring about 60 yrs ago. This fire left deep scars on most of the living Douglas-fir trees on the site and evidently killed others.

Douglas-fir appeared vigorous, with the exception of four badly fire-scarred individuals at Site 2. Two of these proved to have rotten heartwood. Reproduction of this species was abundant and vigorous on all plots. Ponderosa pine trees appeared vigorous, but reproduction was sparse. The lodgepole pine at Site



FIG. 3. *Pseudotsuga/Calamagrostis* stand on a relatively dry site, Tranquille Forest.



FIG. 4. *Pseudotsuga/Calamagrostis* stand on a more mesic area than that shown in Figure 3. *Shepherdia canadensis* is the principal shrub.

2 was low in vigor, and reproduction was absent. The number of dead trees averaged 1 *Pseudotsuga* per plot at both sites, and 1 *Pinus contorta* and 6 *Salix* per plot at Site 2.

The data for height, age and diameter of *Pseudotsuga* given in Table 6 are somewhat misleading due to the influence of fire-injured trees. Actually the average height of the overstory trees was 90 ft at Site 1 and 87 ft at Site 2. The average age of all sound trees was 234 yrs and their average d.b.h. was 22.3 in. The number of dominant trees for which age could be determined satisfactorily was too small for reliable determination of site indices.

The number of trees calculated on an acreage basis with the smaller specimens omitted, was 192 per acre, with an average spacing of 15 ft per tree. The average basal area of 227 sq ft per acre was greater than for any of the other communities studied.

A check was made on a few of the larger individuals of Douglas-fir scattered over the Tranquille Forest study area. For 11 such trees the age ranged from 150 to 300 yrs or more, the heights from 87 to 114 ft, and the d.b.h. from 23.7 to 40.5 in. It is

evident from these data that *Pseudotsuga menziesii glauca* in this area does not approach the proportions attained by the coastal form.

The shrub cover (Table 4) consisted of a few large plants of *Shepherdia* with a lesser amount of *Amelanchier*. In addition there was a thin stand of lower shrubs, principally *Rosa* and *Spiraea*. *Rosa* averaged about one plant per sq m while *Spiraea* averaged only one-third plant for the same area. The principal difference in the shrub cover of the two sites lay in the greater abundance of *Shepherdia* at Site 2 where there were 16 plants per 100 sq m as compared to 3 plants per 100 sq m at Site 1. This difference was in accordance with a generally observed abundance of *Shepherdia* on the more mesic sites in the zone, irrespective of the type of tree cover. *Shepherdia* was also more vigorous at Site 2, averaging 50 in. in height as compared to 22 in. at Site 1. *Amelanchier* was low in stature at both sites, averaging 14 in., but this appeared due to grazing use rather than lack of vigor.

The herbaceous cover (Fig. 5) was clearly dominated by *Calamagrostis rubescens* which had a frequency of 100% at both sites and constituted about 70% of the herbage yield. *Linnaea* and *Arctostaphylos* were also well represented. Only 7 vascular species at each site had frequencies of 20% or more (Table 5). The principal difference between the two sites was the higher frequency of *Linnaea* and *Arctostaphylos* at Site 2.

The yield data (Fig. 2) indicate the predominance of grasses and sedges, mainly *Calamagrostis rubescens*, with a much smaller amount of *Carex richardsonii*. Total herbage and shrub yields were relatively low and in the case of forbs particularly may be somewhat lower than the average for the type. While neither site was under any appreciable grazing pressure at the time of the study, there had been heavy grazing at Site 1 a few years previous and this may have decreased the amount of the more palatable forbs.

The moss-lichen layer consisted mainly of 2 or more species of moss (*Brachythecium*) and 2 species of foliose lichen (*Peltigera*). Also occurring on many sites but with lower frequencies were *Polytrichum juniperum*, *Calliergonella schreberi* and *Cladonia gracilis*. While better developed than in the seral communities of the zone, the moss stratum was still relatively sparse.

THE PINUS/CALAMAGROSTIS ASSOCIES

This community, which currently occupies the major portion of the Douglas-fir zone on the Tranquille Forest was sampled at 3 sites. Site 1 is located on a nearly level bench at an elevation of 3700 ft above sea level. The soil profile resembles closely that described earlier in this paper. The A₂ horizon is of loam texture, while the B₂ is clay loam. The total depth of solum is about 26 in., with rocks dispersed throughout.

Site 2 represents a slightly more mesic habitat,



FIG. 5. Square meter sample plot in *Pseudotsuga/Calamagrostis* association. The herbaceous layer, dominated by *Calamagrostis rubescens*, is relatively sparse.

on an east slope at an elevation of about 3800 ft. The soil profile is similar to that found at Site 1, but slightly rockier.

Site 3 contained a mature stand of lodgepole, one of relatively few in the study area. The elevation is 3700 ft, on a northwest slope of about 10%. The soil is finer textured and less rocky than that found at Sites 1 and 2. The A_2 horizon is also better developed than at the other two sites.

The data for tree cover are summarized in Table 7. *Pinus contorta* was dominant on all sites (Fig. 6) but most strikingly so in the two older stands. Populus was common only at Site 1, and was represented mainly by suppressed individuals. Dead trees of Pinus averaged 3.7 per plot at Site 1, 3.0 at Site 2 and only 1.0 at Site 3. At Site 1 there were also 2.7 dead trees of Populus and 1.0 of Salix per plot. The high percentage mortality of Populus and Salix at Site 1, together with the suppressed condition of the remaining live Populus specimens, indicates a successional trend from a somewhat mixed stand to one dominated almost exclusively by Pinus. The nature of the stands at the two older sites (2 & 3) and observations elsewhere in the zone confirm this trend. A similar situation was reflected in tree reproduction. This was relatively sparse at all sites, but was confined to Pinus at Sites 2 and 3. Even at Site 1 where reproduction of Populus and Salix was present, that of Pinus and *Pseudotsuga* appeared much more vigorous.

The trees at Site 1 represent the age class prevailing over much of the study area and originating after widespread fires in the 1880's. Forty-five percent of the living pines at Site 1 fell in the 60-64 yr age class, 34% in the 50-59-yr age class, and the remainder were scattered among the younger age classes. A few survivors of the fires were found in the area. One of these, on Site 1, was 58 ft high, 11 in. in d.b.h. and 77 yrs old, with conspicuous fire-scars on the base. Such trees were easily distinguished from the general population due to their broader crowns and the presence of live branches low on their trunks.

TABLE 7. Data for tree stands on 3 sites in the *Pinus/Calamagrostis* associes, *Pseudotsuga* zone, Tranquille Forest.

Species	Site	No. INDIVIDUALS		Average Tree Height (Feet)	Average Tree Age (Years)	Average d. b. h. (Inches)
		(Per 100 M ²) Trees	Reprod. ¹			
<i>Pinus contorta</i>	1	23	2.2	45	58	5.1
	2	24	4.0	54	74	4.8
	3	11	2.0	65	135	8.0
<i>Populus tremuloides</i> ...	1	5	14.0	28	56	2.6
	2
	3

¹In addition to the above, reproduction included 0.5 *Pseudotsuga menziesii* and 3.5 *Salix* per plot at Site 1.



FIG. 6. *Pinus/Calamagrostis* stand dominated by 60-yr old *Pinus contorta* and a well-developed herbaceous cover in which *Calamagrostis rubescens* is the principal species.

Site 2 is on an area affected by an earlier fire, which occurred about 1856. The stand at Site 3, while older, also gave evidence of its origin following fire. Each of the sites was located within sizeable areas of the same age-class, and in each case, Douglas-fir was absent or represented by a few old trees which showed the scars of one or more fires.

The number of trees of Pinus was fairly constant from plot to plot, at Sites 1 and 2. The average of 23.5 per 100 sq m equals 950 trees per acre, or an individual spacing of approximately 7 x 7 ft. Stands of pinus in the 55-80-year-old age class in the Tranquille Forest were rather uniform, and approximated this density throughout. The stand at Site 3 showed the characteristic thinning of mature stands.

The average height of individuals comprising the overstory was 50, 67 and 76 ft at average ages of 59, 85 and 138 yrs respectively. The average basal area at the three sites was 143.3, 158.9 and 141.6 sq ft per acre respectively for Pinus alone, with an extra 9.2 sq ft for Populus at Site 1. Total basal areas are well above those recorded for the Populus-dominated sites.

Many stands of *Pinus contorta* were severely devastated by bark beetles (*Dendroctonus* and *Ips* spp.)

during the 1930's. Tree mortality ranged up to 95%, opening up many stands for reproduction. On most of these areas seedlings of *Pinus* were abundant at the time of the present study and in some cases reproduction of *Populus* also. A sample plot in this type was established close to Site 1, on an area of similar soil and topography. Here the tree cover on a 100 sq m plot consisted of 4 saplings of *Pinus*, averaging 10 ft in height, 14 yrs in age and 1.3 in. d.b.h. Reproduction included 43 *Pinus* averaging 34 in. in height, 29 *Populus* averaging 18 in. tall, and 1 *Pseudotsuga* 12 in. in height.

The shrub layer was poorly developed on all three sites, and this was generally true of the *Pinus-Calamagrostis* community over the whole region. *Rosa* and *Spiraea* were fairly abundant but the individual plants were small. The principal shrub was *Shepherdia canadensis* which averaged 34 in. tall with considerable coverage due to the large diameter of the individual plants. In general the shrub stratum was similar to that of the *Pseudotsuga*-dominated stands, the main difference being a greater abundance of *Spiraea* and lesser amount of *Amelanchier* in the *Pinus* community. There was some indication of a decline in the relative amounts of *Rosa* and *Spiraea* in the more mature *Pinus* stands, while *Shepherdia* tended to increase somewhat in abundance and cover. *Pachistima myrsinites* and *Vaccinium membranaceum*, while occurring less commonly than the species noted above, were characteristic members of the community.

The herbaceous cover was clearly dominated by *Calamagrostis rubescens*. The other principal species included *Carex richardsonii*, 4 species of forbs and 4 dwarf shrubs. The forbs, *Lupinus*, *Lathyrus*, *Fragaria* and *Arnica* were about equally important at each of the three sites, and showed a high degree of constancy throughout this community. There was more variability in the distribution of the shrubby species. *Linnaea* and *Arctostaphylos* were represented throughout, with the latter generally less common and varying more in relative amount from site to site. *Vaccinium caespitosum* was patchy in its distribution, and was best represented in the 2 younger stands, at Sites 1 and 2. Overall, it occurred on 60% of all *Pinus* dominated plots. *Pyrola* (*P. secunda* and *P. asarifolia*) was best represented at Site 3, but occurred on all of the intensive study sites and on a high proportion of all plots in *Pinus*-dominated stands.

The yield data (Fig. 2) indicate a considerably higher production of forbs and grasses than was obtained in the *Pseudotsuga* association.

The moss-lichen cover consisted chiefly of *Brachythecium* and *Peltigera*. It was similar in composition but slightly sparser than in the *Pseudotsuga* stands.

THE POPULUS/CALAMAGROSTIS ASSOCIATES

Detailed studies were made at 2 sites representing the major phases of this community found on the Tranquille Forest. Site 1 is located on a 5° south

slope at an elevation of 3100 ft, in the lower portion of the Douglas-fir zone. The soil is of loam texture and generally similar to that described earlier. The principal distinguishing feature is the presence of a distinct lime layer at a depth of approximately 33 in. This feature was found only in relatively xeric sites on the lower fringe of the Douglas-fir zone and was not found in the other sites studied in 1947 to 1948. Site 2 is a more mesic habitat located on a slight southeast slope at an elevation of 3650 ft. The soil profile resembles that found at Site 1, but shows no layer of lime accumulation.

Data for the tree stands are summarized in Table 8. Both sites were occupied by virtually pure stands of *Populus*, but the density of this species was greater at Site 2. The number of dead trees of *Populus* averaged 1 per plot at Site 1, and 5 at Site 2.

TABLE 8. Data for tree stand on 2 sites in the *Populus/Calamagrostis* associates, *Pseudotsuga* zone, Tranquille Forest.

Species	Site	No. INDIVIDUALS		Average Tree Height (Feet)	Average Tree Age (Years)	Average d. b. h. (Inches)
		(Per 100 M ²) Trees	Reprod. ¹			
<i>Populus tremuloides</i> ...	1	16	5	37	53	4.8
	2	27	..	39	60	3.8
<i>Pinus contorta</i>	1	1	1	10	14	1.3
	2	..	1

¹In addition to the above, reproduction included 5 *Pseudotsuga menziesii* per plot at Site 1 and 3 *Salix* at Site 2.

Tree reproduction at Site 1 was noticeable for the presence of vigorous *Pseudotsuga* seedlings averaging 42 in. in height (Fig. 7). *Populus* reproduction was equally abundant, but the individuals were small (aver. 7 in.) and lacked vigor. The few *Pinus* seedlings found at each site were vigorous. The nature and relative vigor of tree reproduction indicated a successional trend towards coniferous species, especially *Pseudotsuga*.

Additional data on this successional process were obtained by counts of all trees and tree reproduction in a half-acre enclosure in which Plot 1, Site 1 was located (Table 9).

These data confirm the trend suggested by the reproduction figures in Table 8 and give some idea of rate of succession. The increase for tree reproduction in the 12-yr interval was 600% for *Pseudotsuga* compared to 75% for *Populus* and virtually none for *Pinus contorta*. While the number of Douglas-fir seedlings was still relatively low (120 per acre), the rate of increase indicated that this deficiency might soon be overcome.

The scarcity of *Pseudotsuga* seedlings at Site 2 appeared due to lack of a seed source, since no trees of reproductive age occurred in the immediate vicinity. At Site 1 a large relict Douglas-fir was situated about 100 yds from the study site.

The heights of overstory individuals of *Populus* averaged 43 ft at Site 1 and 53 ft at Site 2, with average ages of 60 and 62 yrs respectively. The site



FIG. 7. *Populus/Calamagrostis* associates with relatively open stand of *Populus tremuloides* and vigorous reproduction of *Pseudotsuga*.

TABLE 9. Changes in tree stand and reproduction in half-acre exclosure in *Populus/Calamagrostis* associates, Tranquille Forest, 1935-1947.

Species	No. of live trees		No. of dead trees		Reproduction nos.	
	1935	1947	1935	1947	1935	1947
<i>Populus tremuloides</i> ...	209	171	5	23	139	244
<i>Pinus contorta</i>	6	10	1	..	12	13
<i>Pseudotsuga menziesii</i> ..	1	1	10	60
<i>Pinus ponderosa</i>	1

index values of 40 and 46 at 50 yrs place Site 1 in Class 3 and Site 2 in Class 2 according to the system of Baker (1925). Class 2 stands are described by Baker as including most of the stands of good quality in central Utah.

Ring counts at Site 1 revealed 2 age groups of trees, one centering on 60 yrs and the other around 50 yrs. While the spread in computed age within each group might be attributed to errors in counting, the difference between groups appeared too great to be caused in this manner. Only a few of the younger group had attained dominant height. The cause of this phenomenon of 2 major age groups was not determined. No such situation was detected at Site 2, where the main age group ranged from 58 to 64 yrs with no distinct younger class present.

The open nature of the *Populus* stands is indicated by the total basal area figures of 84.8 and 95.2 sq ft per acre Sites 1 and 2 respectively. Small average diameter and low tree density both contributed to giving the aspen stands the lowest basal area per plot of the communities studied.

The sparse shrub stratum showed marked differences in species composition between the 2 sites. At Site 1 the principal shrubs were *Amelanchier* and *Symphoricarpos albus*. At Site 2, the most important species was *Shepherdia canadensis*. Due to the large size and vigorous growth of the individual clumps, this species was more important than the

abundance data indicate. *Rosa* and *Spiraea* were moderately abundant at both sites, but the individual plants were low in stature (aver. 12 in.) and in foliage cover. The more extensive studies made in 1938-1939 showed that *Symphoricarpos* occurred on 50% of all *Populus*-dominated plots, but was abundant on only one-third of them. These latter sites were all in the lower and drier portion of the Douglas-fir zone.

The herbaceous stratum consisted of a well-developed stand of herbs and dwarf shrubby species, with *Calamagrostis rubescens* clearly dominant (Fig. 8). Plant density and vigor of growth combined to give the herbaceous layer a considerably greater production than in the other communities (Fig. 2). Forbs in particular were more numerous and vigorous, with *Lathyrus*, *Vicia*, *Lupinus*, *Aster*, *Fragaria* and *Arnica* most important.



FIG. 8. Undercover vegetation on a square meter plot in the *Populus/Calamagrostis* associates. Note dominance of *Calamagrostis rubescens* and abundance of forbs.

As in the case of the shrub stratum, differences in composition between sites occurred in the herbaceous and dwarf shrub vegetation. *Galium*, *Hieracium umbellatum*, *Taraxacum*, *Viola* and *Berberis* were better represented at Site 1, while *Thalictrum*, *Aster ciliolatus*, *Arctostaphylos* and *Linnaea* were much better represented at Site 2.

In addition to differences in species composition between the 2 sites, there were differences in yield of herbs and shrubs. The data for 1947 showed a total herbage yield of 79.5 gm per sq m for Site 2 as compared to 43.7 gm at Site 1. The order was reversed for shrub production, but total production from the yield plots was 53% greater at Site 2.

The moss-lichen layer was sparse at both sites and in the community generally. It was represented chiefly by *Brachythecium*, with lichens virtually absent.

CONIFER/POPULUS/CALAMAGROSTIS STANDS

As might be expected in seral communities produced as the result of fire, considerable variability

occurred. Over the bulk of the area, however, the tree stands were dominated by either *Pinus contorta* or *Populus tremuloides*, usually with little or no *Pseudotsuga* present. Some mixed stands did occur, however, and one of these, covering an area of about 200 acres, was chosen for study. The principal objectives here were to compare the age and development of the 3 major tree species, and to study the effects of a mixed coniferous and deciduous stand upon the undercover vegetation (Table 10).

TABLE 10. Data for tree stand on 5 plots in mixed conifer/Populus/Calamagrostis stand in the Pseudotsuga zone, Tranquille Forest.

Species	No. INDIVIDUALS		Average Tree Height (Feet)	Average Tree Age (Years)	Average d. b. h. (Inches)
	(Per 100 m ²) Trees	Reprod.			
<i>Pinus contorta</i>	8.6	...	41.0	44	5.0
<i>Pseudotsuga menziesii</i>	7.2	2.4	39.5	40	5.3
<i>Populus tremuloides</i>	8.6	2.8	33.0	47	3.4
<i>Salix</i> spp.	0.8	5.2	19.0	...	2.0
<i>Pinus ponderosa</i>	0.6	0.4	25.5	27.5	3.2

The site chosen for study is located at an elevation of 3400 ft, on a gentle southwest slope. The soil profile is relatively deep and fine-textured with few stones. Edaphically, the site is superior to most of those studied in the Tranquille Forest.

The number of dead trees per plot was small for the conifers (*Pinus* 0.4, *Pseudotsuga* 0.2) but averaged 4.8 for *Populus* and 1.0 for *Salix*.

Populus, although relatively abundant, was inferior to the conifers in height and vigor. The aspen also had a heavier mortality rate, along with a high proportion (one-third) of live trees with rotten centers. Reproduction of this species was lacking in vigor, while that of *Pseudotsuga*, although less abundant, was highly vigorous.

The trees forming the overstory averaged 51.5 ft in height at age 43 and consisted almost entirely of *Pinus contorta* and *Pseudotsuga*. Most individuals of *Populus* had failed to reach overstory height despite a slight advantage in age.

Age counts showed a maximum of 52-yrs for *Pinus*, 55 for *Pseudotsuga* and approximately 60 for *Populus*. The age of the 12 largest and oldest specimens of *Populus* possessing sound heartwood ranged from 57 to 60 yrs. It appears that aspen was the most important tree species on the site for approximately 3 decades following the fire. *Pinus* and *Pseudotsuga* then gradually forged ahead and occupied nearly all of the crown space. Present trends in reproduction indicate that if the stand is undisturbed by fire or other destructive influence, *Pseudotsuga* will increase in importance at the expense of the other tree species.

A noticeable feature of this site was the presence of several large specimens of *Pseudotsuga* within 200 to 300 yds. Evidently this situation was responsible for the excellent reseeded of this species which had occurred on the area. No relict specimens of lodgepole pine or aspen were seen in the vicinity.

Total basal area averaged 121.7 sq ft per acre, less than the average for the *Pinus/Calamagrostis* community and more than that found in the *Populus/Calamagrostis* type. Tree density was similar to that found in the *Pinus contorta* stands of comparable age (Sites 1 and 2, Table 7).

The shrub cover was sparse, with *Amelanchier* and *Shepherdia* the principal species. The former species averaged 18 in. in height on 3 plots protected from livestock grazing and only 12 in. on 2 grazed plots. *Shepherdia* averaged 22 in. and showed no difference due to grazing treatment. *Rosa* and *Spiraea* were more abundant than in the other communities, but their stature was low and foliage cover small.

The herbaceous stratum showed strong dominance by *Calamagrostis rubescens* with *Lathyrus*, *Arnica* and *Viola* all occurring in considerable amounts (Table 5). As a class, forbs produced less than in the *Populus/Calamagrostis* type, but nearly as much as in *Pinus/Calamagrostis*. The content of dwarf shrubby species was relatively low, with *Arctostaphylos* and *Berberis* the principal species. Total shrub production was lower than in the *Populus* or *Pinus* communities.

The moss-lichen layer was extremely sparse, resembling that of the *Populus/Calamagrostis* type.

RELATIONSHIPS OF TREE COVER TO UNDERSTORY VEGETATION

Two aspects of this relationship encountered in the present study were the effect on the kind and amount of undercover vegetation produced by (a) different densities of coniferous trees and (b) stands of coniferous species compared to broad-leaf, deciduous trees. Data from the regular community study plots, together with a small amount of additional sampling, supplied a limited amount of information concerning these two phases.

In the study of coniferous stand density in relation to understory vegetation, a *Pseudotsuga* stand with dense reproduction and a *Pinus contorta* site with the tree stand largely killed by bark beetles were given special study.

One major sample plot was established in a dense stand of *Pseudotsuga* reproduction. The tree stand consisted of a dense cover of 45-to 50-yr-old *Pseudotsuga* with scanty undergrowth, and was selected as typical of numerous stands of this nature found scattered throughout the zone (Fig. 9). Sampling was done as in the regular community studies. The live tree stand was found to consist of 50 *Pseudotsuga* and 8 *Populus*, with 6 dead specimens of the former and 2 of the latter. Reproduction was confined to 14 *Pseudotsuga*, averaging 88 in. in height. Trees of this species averaged 22 ft in height, 48 yrs, and 2.6 in. in d.b.h. *Populus* averaged 32 ft, 46 yrs, and 3.8 in. in diameter. Total live tree density was 58 per 100 sq m, compared to 25.6 in the "mixed" community (Table 9) which appeared comparable in age and site characteristics. Total basal area was 121 sq ft



FIG. 9. Dense young *Pseudotsuga* stand, showing poor growth of 50-yr old trees and sparse nature of the under-cover vegetation.

per acre, the same as in the "mixed" stands (Table 3).

The shrub layer consisted of 4 plants of *Amelanchier*, and a sparse stand of *Rosa*. The herbaceous cover was dominated by *Calamagrostis rubescens* with *Fragaria*, *Linnaea*, *Lathyrus*, and *Berberis* the most common associated species. Only the 5 last-named plants and *Rosa* had frequencies of 20% or more. By comparison, the mature *Pseudotsuga* sites had 9 species with frequencies of 20% or greater, and the *Pinus contorta* sites contained 10 such species. Total yield of herbs and shrubs averaged 11.4 gm per sq m, compared to 20.1 gm for the mature *Pseudotsuga* stands.

Further evidence concerning the effect of *Pseudotsuga* reproduction on undercover vegetation was obtained on a site which had been logged heavily about 30 yrs ago. The area was occupied by dense thickets of Douglas-fir reproduction interspersed with openings of various size. Here 2 sets of three sample plots, each 1 sq m in size, were established along lines running from openings into thickets. Plot 1 of each series was located in the center of an opening about 18 m in diameter, Plot 2 in an opening about 3 m across and Plot 3 in a stand of *Pseudotsuga* 1-3 in. in d.b.h. and averaging 2 trees per sq m.

Counts and cover estimates made on the vegetation of these 3 pairs of plots showed marked differences among them. Plots 1 had what might be considered a normal cover for the *Pseudotsuga*/*Calamagrostis* community. *Calamagrostis rubescens* was the dominant herbaceous species, while *Carex richardsonii*, *Aster conspicuus*, *Fragaria glauca* and other forbs occurred in considerable numbers, and *Arctostaphylos uva-ursi* occupied an estimated 5% of each plot. In the second series of plots, the species composition was somewhat the same, but the abundance of *Calamagrostis* was only 20% of that in Plots 1, and the other herbaceous species were reduced to an even greater degree. The moss and lichen cover was well developed and occupied much more area than on Plots 1, although the species composition was not

altered noticeably. On Plots 3, where the tree cover was most dense, herbaceous species were almost lacking, and even the moss-lichen cover was reduced, with *Cladonia* and *Peltigera* represented, but without *Brachythecium* which was so evident at Plots 2.

Similar differences in sites supporting different amounts of young coniferous tree cover were observed in many portions of the study area.

In the *Pinus*/*Calamagrostis* community one sample plot was established on an area where most of the tree stand had been killed by bark beetles. In other respects the site was similar to Site 1 of the regular community study. The tree stand on the beetle-affected site consisted of 4 *Pinus contorta* averaging 10 ft in height, 14 yrs old and 1.3 in. in d.b.h. Tree reproduction was abundant and vigorous, with 43 *Pinus* averaging 14 in. and 29 *Populus* averaging 18 in. in height. The shrub and herbaceous cover was well developed on this plot, with an average yield of 69 gm per sq m compared to 46.5 gm for the normal *Pinus*-dominated stands. The largest difference was in yield of grasses and sedges, mainly *Calamagrostis rubescens*, but total forb yields were 40% and shrub production 23% greater. The frequency plots showed *Rosa*, *Spiraea*, *Arnica* and *Lathyrus* to be approximately twice as well represented in the insect-killed as in the average of adjacent stands not affected by the beetles, while *Arctostaphylos* and *Pyrola* spp. had higher frequency indices in the latter type.

Consideration of possible differences in kind and amount of understory vegetation between conifer-dominated and deciduous tree stands involved comparisons of constancy, frequency and yield data for all study sites. Preliminary examination of species constancy and frequency data indicated that differences between the two conifer-dominated communities were slight, but that larger differences existed between these and the aspen-dominated stands. To check further on this matter an analysis was made of the data for constancy on all sites, including those established in 1938 to 1939 and for frequency on the sites studied in 1946 to 1949.¹

An attempt was made with these data to separate the principal undercover species according to their degree of fidelity in conifer- or aspen-dominated communities according to the classification of Braun-Blanquet (1932).

The results of this analysis are as follows:

I. Conifer-dominated communities (*Pseudotsuga*/*Calamagrostis* and *Pinus*/*Calamagrostis*).

Exclusive species—none could be placed here.

Selective species—*Pachistima myrsinites*, *Vaccinium membranaceum*, *Chimaphila umbellata*, *Goodyera oblongifolia*, *Hieracium albiflorum*, *Pyrola asarifolia*, *Cladonia gracilis*, *Peltigera canina*, *P. aphthosa* and *Polytrichum juniperum*.

Preferential species—*Linnaea borealis*, *Vaccinium caespitosum*, *Pyrola secunda*, *Bachythecium* spp.

¹ A list of all species encountered in the entire study period (1938-1948) together with the constancy data has been prepared in dittoed form and will be supplied upon request.

Indifferent species—*Amelanchier alnifolia*, *Shepherdia canadensis*, *Spiraea betulifolia*, *Juniperus communis*, *Arnica cordifolia*, *Aster conspicuus*, *Astragalus serotinus*, *Calamagrostis rubescens*, *Carex richardsonii*, *Fragaria glauca*, *Lathyrus ochroleucus*, *Lilium parviflorum*, *Lupinus glacialis*.

II. Aspen-dominated community (*Populus*/*Calamagrostis*)

Exclusive species—none.

Selective species—*Agropyron subsecundum*.

Preferential species—*Symphoricarpos albus*, *Berberis repens*, *Achillea lanulosa*, *Aster ciliolatus*, *Galium boreale*, *Hieracium umbellatum*, *Taraxacum officinale* and *T. laevigatum*, *Thalictrum occidentale*, *Vicia americana* and *Viola adunca*.

The constancy data, representing the largest number of sites, were considered most valuable in determining species of relatively high fidelity ("selective species"), while the frequency data were helpful in indicating "preferred species" which occurred commonly in both types of community, but with much greater frequency in one or the other.

From this analysis it seems clear that differences in understory species composition between the conifer and aspen-dominated stands do exist. These differences are largely quantitative in nature, however, with no "exclusive species" and only a few "selective species" occurring in either type. The most abundant understory species occurred more or less equally under the two types of forest cover.

Another source of information regarding the overall effect of tree stands on their undercover vegetation was provided by the yield data obtained on the herbaceous and smaller shrubby species. These data (Fig. 2) show distinct differences among communities, with the *Populus*-dominated stands ranking highest, the *Pinus contorta* second and the *Pseudotsuga* association lowest in this regard. This order of rating is opposite to that for average tree basal area per acre (Table 3). This is to be expected, since tree basal area is generally considered to be one of the better measures of the total influence of tree stand upon a site (Kittredge 1948, p. 30).

Total annual production of understory vegetation recorded in the present study, including that of a beetle-killed *Pinus contorta* site and an area occupied by a stagnated stand of 50-year old *Pseudotsuga* represent a wide range of values. The two extremes were the *Populus* community with an average of 72 gm per sq m and the dense young *Pseudotsuga* stand with 11.4 gm. The yield from the beetle-killed *Pinus* site was almost equal to that for the *Populus* stands, and about 50% greater than for comparable sites occupied by a normal stand of *Pinus*. Differences of considerable magnitude in long-leaf pine stands in Alabama have been reported by Gaines *et al.* (1954). These authors discovered a significant curvilinear relationship between tree basal area and herbage production, but other factors including tree grouping and soil characteristics were found to be involved also.

Detailed investigation of the factors responsible for the effects of tree stand on understory vegetation was not attempted in the present study. Presumably competition for soil moisture is involved, in view of the limited annual precipitation in the *Pseudotsuga* zone and the frequent occurrence of moisture deficiencies in the surface soil layers during July and August.

It was thought that solar radiation might also be a limiting factor for undercover vegetation, especially in the denser tree stands. Preliminary observations were made at 4 sites representing the 3 principal communities studied plus a dense stand of young *Pseudotsuga*. Light measurements were made in the manner described by Shirley (1945) using photoelectric exposure meters to record the light reflected from sheets of white paper placed on the ground. Fifty to 100 readings were taken at each site, at intervals of 1 m along transects of 25 observations each. The transects were established on the center line of the regular community study plots. The results, converted to percentages of full sunlight, gave averages of 40, 38 and 28% for the *Populus*, *Pinus contorta* and *Pseudotsuga* communities and 10% for the dense young *Pseudotsuga* stand. These data indicate the presence of a denser crown canopy in the *Pseudotsuga* stands than in the two seral communities, but not any actual deficiency of solar radiation. Only in the dense young *Pseudotsuga* stand did light intensity drop to a point which might be considered definitely limiting for plant growth.

BIOTIC FACTORS

Grazing, fire, insects and pathogenic fungi all gave evidence of being significant factors in one or more of the plant communities found in the study area.

The effects of grazing were studied over the period 1935 to 1947 as part of the research program of the Kamloops sub-station. The results of these studies will be reported in a subsequent publication. Briefly, it was found that *Calamagrostis rubescens* and several other species preferred by cattle declined in abundance and vigor under heavy grazing use. The plants most affected included *Aster conspicuus*, *Lathyrus ochroleucus*, *Vicia americana* and *Castilleja* spp. Reproduction of *Pseudotsuga*, *Pinus contorta* and *Populus* was also affected on overgrazed areas. Under moderate grazing use little or no change in undercover vegetation or tree reproduction could be detected. Use by wildlife (deer, moose, rodents and rabbits) was also evident, especially in areas where livestock were excluded. Generally, grazing by wildlife did not appear excessive, but winter use of *Populus* and *Salix* shoots was heavy in some areas.

The drastic effects of past fires on the vegetation of the area have been discussed earlier. Due to improved controls, fire has been much less prevalent during the past few decades than in earlier times.

The most striking example of insect damage was the heavy mortality of *Pinus contorta* and *Pinus ponderosa* due to bark beetles, chiefly *Dendroctonus* and *Ips* species. These beetles were extremely active

in the study area from 1930 to 1935 and affected the extensive stands of *Pinus contorta* to a marked degree (Fig. 10). On areas of marked *Pinus* mortality the

of vegetation-soil relationships in southern Interior British Columbia (Spilsbury & Tisdale 1944) and by observations made over much of the interior region.



Fig. 10. Deadfall formed by beetle-killed *Pinus contorta* in the *Pinus/Calamagrostis* associates of the Pseudotsuga zone. The fallen trees, many of which lie well off the ground, persist for many years before rotting and constitute a serious fire hazard as well as a deterrent to grazing use.

undercover vegetation was stimulated to a moderate degree. Increased numbers of *Populus* were observed on some of these areas, but in the main reproduction consisted principally of the pine.

In stands of *Populus* a cerambycid beetle, *Saperda* sp. appeared to be of considerable importance, especially on sites of poor quality. The larvae of this insect bore through the aspen stems and produce numerous openings to the outside of the trunk. On several heavily infested stands checked in 1946-47 about half the middle-aged aspens were dead or dying as a result of attacks by these beetles. Baker (1925) reports severe damage to aspen by *Saperda calcarata* in Colorado and Lynch (1955) found *Saperda* to be an important influence in poor quality aspen stands in northwestern Montana.

The aspen stands were also affected by pathogenic fungi, of which the principal species appeared to be heart rot, *Fomes ignarius*, which was common on the poorer sites. Most of the badly affected trees were 50 yrs of age or more, but some as young as 30 yrs showed the beginnings of decay. Heart rot and associated fungi appeared to be playing a considerable part in the destruction of aspen stands in the lower part of the Douglas-fir zone. *Populus* on better quality sites throughout the zone was much less affected by fungi.

ECOLOGICAL AND GEOGRAPHICAL RELATIONSHIPS

The relationship of the vegetation studied in the Pseudotsuga zone of the Tranquille area to that of other areas in the same zone and to adjacent vegetation zones was studied in the course of a general survey

THE PSEUDOTSUGA ZONE IN INTERIOR BRITISH COLUMBIA

Relationships within the Pseudotsuga zone were studied mainly in the area lying south of Quesnel (latitude 53°) and embracing types "M-1" and "M-2" of Halliday (1937). The localities checked included Williams Lake, Riske Creek, Canoe Creek and Pavilion Mountain in the Middle Fraser (Cariboo) region; Fish Lake 25 mi southwest of Kamloops and several areas in the Nicola and Okanagan Valleys extending to the extreme southern portion of the interior region. At each site, notes were made on site factors and dominant species and the soil profile examined. In most cases a full species list was also made.

Comparison of the results from these observation plots with the results from the detailed studies on the Tranquille area shows a high degree of similarity. Especially notable features include the consistent dominance of *Calamagrostis rubescens* and the high constancy values for *Rosa*, *Spiraea* and many of the common forbs.

McLean & Holland's (1956) recent description of the vegetation of the Upper Columbia Valley includes a *Pseudotsuga/Calamagrostis* association as the climatic climax of the Douglas-fir zone in that area. The description of this community agrees closely with the *Pseudotsuga/Calamagrostis* association of the Tranquille Forest and adjacent areas.

Another source for comparison is provided by the data of Kujala (1945), who recorded species occurrence and relative cover on plots of uniform size. Kujala's "*Arctostaphylos-Calamagrostis* type" appears to be identical with the *Pseudotsuga/Calamagrostis* association described in the present paper. The data from all 10 sites in this "*Arctostaphylos-Calamagrostis* type" distributed across the southern portion of interior British Columbia agree closely with those of the present authors.

It appears that the *Pseudotsuga/Calamagrostis* association is widespread in interior British Columbia and marked by a well-defined vegetation, both in the climax and seral stages. The principal species, in approximate order of constancy values, are as follows:

- Trees:* *Pseudotsuga menziesii* (climax), *Pinus contorta* and *Populus tremuloides* (seral).
- Shrubs:* *Rosa gymnocarpa*, *Spiraea betulifolia*, *Shepherdia canadensis* and *Amelanchier* spp.
- Dwarf Shrubs:* *Arctostaphylos uva-ursi*, *Linnaea borealis*, *Berberis repens* and *Vaccinium caespitosum*.
- Herbs:* *Calamagrostis rubescens*, *Fragaria glauca*, *Carex richardsonii*, *Aster conspicuus*, *Arnica cordifolia*, *Goodyera olbongifolia*, *Lathyrus ochroleucus*, *Lupinus glaucialis*, *Astragalus serotinus*, and many species of lesser occurrence.
- Mosses and Lichens:* *Brachythecium* spp., *Cladonia gracilis* and *Peltigera* spp.

No attempt was made in this study to determine possible subdivisions of the *Pseudotsuga/Calamagrostis* community, chiefly because of the localized nature of the detailed sampling. The most evident separation on the basis of undercover vegetation would be one based on the relative importance of *Lupinus glacialis*. This species is frequently the principal forb at higher elevations in the zone, but is rare or lacking in the lower portions. This situation is mentioned by Kujala who states that "a lupine variant could easily be justified." Another possible separation would be one based on the shrub stratum, recognizing an association in which *Symphoricarpos* is the dominant shrub. This variant is represented in the present study only in a seral stage (*Populus/Calamagrostis*, Site 1), and was not observed in climax *Pseudotsuga* stands. The fact that *Symphoricarpos* was found in abundance only under *Populus* and then only in stands occurring along the lower, drier edges of the *Pseudotsuga* zone, suggests that it may represent a forest-grassland ecotone, and in addition may be largely seral in nature. *Populus/Symphoricarpos* vegetation in western Montana and Alberta is described by Lynch (1955) and Kujala (1945) as belonging primarily to the fringe of the *Populus* zone in those areas. Other subdivisions may also be recognized as studies are made on a regional basis.

Despite the widespread occurrence of the *Pseudotsuga/Calamagrostis* association in interior British Columbia, it is not the only climax community which has been recognized in the Douglas-fir zone of this area. In the Kootenay region in the southeastern corner of the Province, a community occurs which corresponds to the *Pseudotsuga/Physocarpus* association of Daubenmire (1952). To date, this vegetation type has not been observed by the authors elsewhere in interior British Columbia. McLean & Holland (1956) have also described a *Pseudotsuga/Agropyron* association on dry sites in the Upper Columbia area.

On sandy soils in the area west of Williams Lake, in the Cariboo region, extensive areas occur in which *Pinus contorta* is the principal tree, and *Arctostaphylos uva-ursi* dominates the undercover vegetation. Further study is needed to determine the relation of this vegetation to the communities described in the present paper.

RELATION TO OTHER VEGETATIONAL ZONES

The Douglas-fir zone over much of southern interior British Columbia, contacts 3 major communities, namely the spruce/fir, ponderosa pine and the Pacific Northwest grassland. The relationship of these zones was studied in some detail on the Tranquille Forest and observations made in other parts of interior British Columbia.

In general, sharp differences in plant cover were found among the zones with only a few species well represented in more than one zone. Among the trees, the most striking example of overlap is furnished by *Pinus contorta*. This species occurred commonly

throughout the Douglas-fir and spruce/fir zones, and was a seral dominant in each. *Shepherdia canadensis* in the shrub layer and *Arnica cordifolia* and *Linnaea borealis* in the herb-dwarf shrub stratum showed ubiquitous distribution less related to seral conditions than in the case of the pine.

In both zones, the character of the understory vegetation was not affected drastically by the replacement of the climax conifers by *Pinus contorta*. As a result, zonal boundaries were evident in the undercover even where *Pinus* formed the dominant tree cover in both zones.

Pseudotsuga, although not occurring on any of the sample plots in the spruce/fir zone, was observed to occur occasionally as a seral species. A similar situation was observed farther north, in the vicinity of Quesnel. Cowan *et al.* (1950) have reported the presence of *Pseudotsuga* along with *Pinus contorta* as seral species on burned areas in the *Picea/Abies* zone near Quesnel.

The presence of *Picea* in fair numbers at middle elevations in the Douglas-fir zone in the Tranquille area at first appeared to represent an unusually deep intrusion of the spruce/fir zone into valley bottom areas. Subsequent examination revealed that the spruce occurring at these lower elevations is not *Picea engelmannii*, but rather *P. glauca*. This latter species has somewhat different ecological affinities and is much more abundant in north-central British Columbia and on the eastern slope of the Rocky Mountains. Sites at the upper margin of the Douglas-fir zone showed some differences in understory vegetation. The shrub cover frequently included *Alnus* sp., and *Pachistima myrsinites* was abundant. *Amelanchier* was scarce or lacking. Among the dwarf shrubs *Linnaea borealis* was more abundant and *Actostaphylos uva-ursi* less common than in the main body of the zone, while *Berberis repens* was rare.

Study of the relationship of the Douglas-fir and ponderosa pine zones in the Tranquille Forest was handicapped by the limited occurrence of the latter community. The ponderosa pine zone reaches its northern limits some 40 mi. north of the study area, and is represented by discontinuous areas situated between the grasslands and the Douglas-fir zone. Douglas-fir mingles with the pine over an ecotone which is often as broad as the *Pinus ponderosa* zone itself.

Pinus ponderosa shows some overlap into the Douglas-fir zone, acting as a seral species after fire, although not to such an extent as do *Pinus contorta* and *Populus tremuloides*. On dry, exposed slopes ponderosa pine showed evidence of persisting well above its normal zonal limits. Elsewhere the usual situation is one of well-grown trees of the pine in stands where tree reproduction consists mainly or entirely of Douglas-fir.

The undercover of the 2 zones shows little similarity. In the Tranquille area, as in much of interior British Columbia, the ponderosa pine zone is represented mainly by the *Pinus/Agropyron* association.

This community occurs where the pine zone directly contacts one of the drier grassland associations, usually the *Agropyron/Poa*. A similar situation has been reported in northern Idaho and Washington (Dauenbire 1952). The undercover of this association contains an abundance of such prairie plants as *Agropyron spicatum*, *Koeleria cristata*, *Antennaria parvifolia*, *Achillea lanulosa* and *Chrysothamnus nauseosus*.

The marked difference in undercover between the *Pseudotsuga* and *Pinus ponderosa* zones is associated with basic differences in soil profile. The soil of the ponderosa zone resembles a grassland type (Spilsbury & Tisdale 1944) while that of the Douglas-fir belongs to the brown podsol group.

Along the contact line of the two zones, dominance of the ground cover by *Calamagrostis rubescens* appeared to be a good indicator of the Douglas-fir zone, regardless of the nature of the present tree stand.

In other parts of the Tranquille area the Douglas-fir zone abuts directly on the *Agropyron/Festuca* association of the Pacific Northwest grasslands (Tisdale 1947). The contact is in most cases a sharp one, lacking any appreciable ecotone.

A limited study of this border was made, particularly to determine whether it may be considered a natural and stable community boundary. In the study area a complex pattern was found, with forest and grassland alternating on areas of rough topography (Fig. 11). Both Douglas-fir and aspen dominate along the forest edge. Detailed observations indicated that *Pseudotsuga* was not invading well-established grasslands, but isolated groves of aspen had become established during the past few decades. These groves occurred either at the edge of the Douglas-fir stands, or in low areas surrounded by grassland. In both cases the aspen had developed by root offshoots from one or a few parent trees. Numerous aspen sucker shoots were found along the edges of both types of grove, but their vigor was low and the mortality rate appeared to be high. Intermediate age classes of aspen were absent along the edge of most groves. The trees themselves were stunted, rarely exceeding 40 ft in height and 12 in. in d.b.h. with excessive taper of the trunk. The prevalence of rotten centers even on relatively young trees made accurate age determination impossible.

Direct invasion of *Pseudotsuga* into grassland was found to be confined to small areas of rocky soil where the grass cover was sparse and lacking in vigor. Here *Pseudotsuga* seemed to be spreading slowly from scattered parent trees. As in the case of *Populus*, the individual trees were dwarfed and branchy.

Although forest appeared to be making a slow, irregular advance on grassland in the cases mentioned above, the boundary appeared relatively stable over most of the area studied, with mature trees located at the extreme edge of the forest. No detailed study was made of the factors involved in limiting the forest edge. Lynch (1955) working in an aspen-grass-



FIG. 11. Contact of *Pseudotsuga* zone and *Agropyron/Festuca* grassland on lower edge of Tranquille Forest. *Populus* and *Pseudotsuga* have invaded the grassland in spots, but the main forest boundaries appear stable.

land border in northwestern Montana found that a deficiency of soil moisture in late summer was the principal factor preventing invasion of *Festuca* grassland by aspen. McMinn (1952) reports marked differences in seasonal soil moisture in the *Festuca/Symphoricarpos* association of eastern Washington and adjacent Idaho as compared to adjacent *Pinus ponderosa* and *Pseudotsuga* dominated communities. It appears probable that a similar moisture limitation is effective in controlling grassland-forest boundaries in southern and central interior British Columbia.

Conditions similar to those described above were observed in the Nicola, Okanagan and Middle Fraser regions of the Province. In parts of the Middle Fraser area *Pinus contorta* appears to be directly invading grassland areas, much as *Populus* does farther south. Overall it appears that the Douglas-fir zone, with aspen and in some cases lodgepole pine as the pioneer species is encroaching upon grassland in limited areas, possibly as a result of decreased frequency of prairie fires. It is known that the Indians of these territories used fire as a means of securing better conditions for hunting, and these fires together with those caused by lightning may have been sufficient to maintain grassland in potential forest areas. In the north-central and northern portions of the Interior a more widespread invasion of grassland by forest appears to be occurring (Brink & Farstad 1949), but this area lies mainly outside the *Pseudotsuga* zone.

SUMMARY AND CONCLUSIONS

The Douglas-fir zone constitutes one of the major plant communities of interior British Columbia, occupying a substantial portion of the interior Plateau System from the southern boundary of the Province north to Latitude 53°. This region, situated between the Coast Range on the west and the Rocky Mountain system on the east, is characterized by rough topography, particularly in the southern portion.

Within the Douglas-fir zone the climate is relatively dry due to the rain shadow effect of the Coast Range. The seasonal distribution of precipitation is charac-

terized by two maximal periods, a major one in May-July and a lesser one in December-January. The soils are of glacial origin and are tentatively classified as belonging to the Brown Podsol group.

Fire, insects, fungi, logging and grazing are important factors affecting the vegetation of this zone, with fire the dominant influence until recently. Mainly as a result of fire, the major portion of the zone is currently dominated by seral tree species, particularly *Pinus contorta* and *Populus tremuloides*.

The present study was made chiefly on the Tranquille Forest near Kamloops, with less detailed observations in other parts of the region. Following a broad preliminary study detailed data were obtained on permanently marked sample plots located in each of the communities recognized.

The climax in the areas studied is the *Pseudotsuga/Calamagrostis* association, with the tree stand dominated by *Pseudotsuga menziesii* var. *glauca* and the understory by *Calamagrostis rubescens*. Mature stands are composed almost exclusively of *Pseudotsuga* and are relatively open, with the trees spaced about 15 ft apart. The trees are smaller than the coastal form of Douglas-fir, seldom exceeding 115 ft in height and 40 in. in d.b.h.

The relatively sparse shrub cover is dominated by *Shepherdia canadensis*, *Rosa gymnocarpa* and *Spiraea betulifolia*. The herbaceous and dwarf shrub stratum is well developed. Important species in addition to the dominant *C. rubescens* include *Arnica cordifolia*, *Aster conspicuus*, *Carex richardsonii*, *Fragaria glauca*, *Lathyrus ochroleucus*, *Arctostaphylos uva-ursi*, *Berberis repens* and *Linnaea borealis*. *Lupinus glacialis*, lacking at lower elevations in the zone, is common to abundant in the higher portions.

The poorly developed moss-lichen layer is characterized by species of *Brachythecium*, *Cladonia*, and *Peltigera*.

The principal seral community is the *Pinus/Calamagrostis* associes. Here the tree cover is more or less even-aged, due to its origin following fire. Mature individuals attain heights of 60-70 ft and diameters of 12 to 18 in. The understory vegetation is similar to that of the *Pseudotsuga/Calamagrostis* association, but somewhat more vigorous and productive.

The second seral type is the *Populus/Calamagrostis*, which is characterized by the most open tree cover and best-developed herbaceous understory of any of the 3 communities. Most of the *Populus* stands are even-aged and apparently have resulted largely from sucker shoots. However, numerous seedlings of aspen have been observed on recently burned areas. The shrub cover varies considerably within this community, with *Symphoricarpos albus* dominant in the drier sites and *Shepherdia canadensis* in the more mesic areas.

Understory vegetation in the zone is strongly affected by the amount, age and kind of tree stand. The amount of herbaceous cover, as measured by clipped plots, is highest in *Populus* stands, intermediate in *Pinus contorta* and mixed conifer-*Populus* stands, lowest under *Pseudotsuga* cover.

Certain differences in species composition occur between the conifer-dominated communities and the *Populus/Calamagrostis* associes. While no species could be classed as exclusive to either group, 11 were rated as selective and 15 as preferential according to the fidelity classification of Braun-Blanquet. The plants classed as selective to conifer-dominated communities include several evergreen species (*Pachistima myrsinites*, *Chimaphila umbellata*, *Pyrola asarifolia*) and several lichens and mosses. All of the species in this conifer-selective group were represented in the *Picea/Abies* zone also.

The vegetation of the *Pseudotsuga* zone is clearly distinguished from that of the *Pinus ponderosa* and *Picea/Abies* zones which contact it in the zonal sequence of forest types. *Pinus ponderosa* acts as a seral species in the lower portion of the Douglas-fir zone, as does *Pseudotsuga* to a limited extent in the *Picea/Abies* zone. *Pinus contorta* is a major seral species in both the *Pseudotsuga* and *Picea/Abies* zones.

Over considerable areas where *Pinus ponderosa* is lacking in the zonal sequence, the *Pseudotsuga* zone abuts directly on the *Agropyron/Festuca* association of the Pacific Northwest grasslands. This boundary is sharp, and for the most part appears stable. In limited areas tree invasions of the grassland is taking place, with *Populus* and to some extent *Pinus contorta* acting as pioneer species and forming groves in local situations favored in regard to soil moisture.

The *Pseudotsuga/Calamagrostis* community appears to constitute the climax over a large part of the *Pseudotsuga* zone. The *Pseudotsuga/Physocarpus* association common in northern Idaho and adjacent Washington occurs in the southeastern portion of the region. Further subdivision of the *Pseudotsuga* zone may be indicated when further studies have been made.

Although present conditions favor establishment of the climax tree cover over the region, there are large areas in which this process will be extremely slow due to lack of a seed source of *Pseudotsuga*. The *Pinus/Calamagrostis* community in particular now extends over large areas in which *Pseudotsuga* is lacking or rare. In such areas this fire-induced disclimax must be considered as a semi-permanent type from the viewpoint of one or two generations at least.

From the limited data presented in this paper, together with the extreme sparseness of the literature, it appears obvious that much further investigation of vegetation and soils is needed in the *Pseudotsuga* zone of interior British Columbia. The great size of the area occupied, and the complexity induced by topographic irregularity, fire and other factors, would seem to make basic studies of the zone an essential requirement for satisfactory solution of land use problems which exist now or are likely to arise in the near future as use becomes more intensive.

These investigations should include synecological studies aimed toward the recognition and description

of all the basic vegetational units comprising the zone. Also needed are long-term successional studies of the effects of logging, grazing, fire and in the case of seral stands, protection from fire. One by-product of the studies outlined would be to provide a clearer picture than is now available of the areas and types to which data obtained on the Tranquille Forest can be applied with validity.

To supplement the research on plant communities and their habitat, there is also need for autecological studies of native species, especially the common shrubs and herbs. Little is known at present of the life-histories of these species or of their reaction to fire, logging disturbance or grazing use.

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VARIATIONS IN COVER, COMPOSITION, PRODUCTION, AND ROOTS OF VEGETATION ON TWO PRAIRIES IN WESTERN KANSAS

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INTRODUCTION

The mixed prairie from Canada to Mexico has been the subject of numerous investigations. Coupland (1950) gave a detailed description of their plant communities in Canadian grasslands. Hanson & Whitman (1938) listed 9 major grasslands based on variations in soil and topography in western North Dakota. Range types in eastern Wyoming and eastern Colorado were recorded by Costello (1944). Hopkins (1951) working on the loessial soils of central Nebraska divided the area into short grass, mixed grass, mid and tall grass, and western wheatgrass communities. In his study on the vegetation of Oklahoma, Bruner (1931) described the mixed prairie and short grass regions. Cottle (1931) described the vegetation of southeast Texas, a part of which was originally dominated by mixed prairie vegetation. These fine studies have covered many of the principal plant communities of the mixed prairie, but they have not included some of the less extensive ones.

Many ecological studies have been made of grasslands of mixed prairies near Hays, Kansas. Albertson (1937) conducted a study of environmental factors and vegetation types of a mixed prairie in this area. With the exception of drought studies over a wide range (Weaver & Albertson 1940a, 1940b; Albertson & Weaver, 1942, 1944, 1946), most of the investigations in western Kansas have been limited to the vicinity of Hays. There are many grasslands in western Kansas, however, that are different from those near Hays, principally because of variation in soil and topography.

Within the general region of the central Great Plains there are many types of mixed prairies. The

study described in this paper was made on prairies in western Kansas, which are a part of the mixed prairie, but which, because of variations in soils, are somewhat different from those studied intensively at Hays, Kansas. The two types of prairies selected for study were found on the Permian redbeds close to Ashland in southwestern Kansas and loessial soils near Atwood in northwestern Kansas. The purpose of this investigation was to collect information on these native prairies found on soil types that are different from those on which other studies have been made. Basal cover and percentage composition of grasses, relative abundance of forbs, forage yields, and root development of important plants were studied on these undisturbed prairies. Effects of different intensities of grazing were also measured. Information of this nature has been used extensively by government agencies in classifying range conditions and in making recommendations for proper use of grasslands. Frequently, however, studies have been made on grasslands found in a limited area and the results have been applied over a much more extensive area. The study presented in this paper should add to the general fund of knowledge on grasslands of western Kansas and point out some of the variations that do exist.

METHODS OF STUDY

Three pastures were selected for study at Atwood, Kansas and three at Ashland. Each of these three pastures was typical of ranges that had been non-grazed, moderately grazed and heavily grazed in both areas. Various criteria have been used for identifying moderate and heavy use. Many range tech-

nicians have identified moderate use as the condition where approximately half of a season's growth is removed by livestock. Heavy use by livestock generally refers to that condition where more than 75% of the season's forage production has been removed. All areas were grazed by beef cattle. Each pasture was divided into sites based on topography. The 4 sites so selected were upland, hillside, sharp breaks, and lowland.

Cover and composition of grasses on both grazed and ungrazed prairies were ascertained by the square foot method described by Voigt & Weaver (1951). This consists essentially of estimating basal cover and percentage composition of grasses in square-foot quadrats located randomly throughout the area sampled. Three hundred (300) square-foot samples were taken on each site of the pastures studied. The average cover and composition of the grasses were then computed for each site.

Number and kinds of forbs were counted in randomly placed 100 square-foot areas. Ten to twenty areas were used on each site of all prairies.

Forage produced on 3 sites of the nongrazed, moderately grazed and heavily grazed prairies at both locations was collected from square foot and square meter areas. Ten square-meter areas and 30 square-foot areas were used to sample each site on a pasture. Quonset-shaped wire cages 4 ft long, 2 ft wide and 2.5 ft high were placed over two square-foot areas to protect them from grazing. Teepee shaped exclosures described by Lacey (1942) were used to protect the meter quadrats. Forage was clipped each month of the growing seasons in 1952 and 1953 on all quadrats, air-dried, weighed and converted to lbs/A. Different locations were used for the 1952 and 1953 clippings. The average production was computed for each site on all prairies.

Root systems of nongrazed and heavily grazed pastures were studied by using the bisect method (Weaver 1919). Long trenches were dug beside plants to be studied and soil was carefully removed from around the roots with ice picks. Diagrams of the root systems were made and photographed.

Scientific names of grasses used in this study are those of Hitchcock & Chase (1950). Nomenclature of forbs follows Gleason (1952) and Harrington (1954). The latter manual was used for plants not included in the former.

CLIMATIC CONDITIONS

This study was initiated at the close of a wet year and continued through two very dry ones. In fact growing conditions at both Atwood and Ashland were below normal throughout the study. Both years had a midseason drought accompanied by other environmental conditions not conducive to plant growth.

In 1952 at Atwood drought started in June and lasted through October; in 1953 it began in May and extended through September. Even though the first year was 3.79 in. below the 18.53 in. normal and the

last year of the study was 0.29 in. above normal, the latter was worse for growth of vegetation. This was true probably because 1953, unlike 1952, was not preceded by a wet year. High temperatures accompanied low rainfall to make the droughts more severe. June was an especially hot month for both years averaging 6.4° F above normal in 1952 and 4.1° F above in 1953.

Ashland had a total rainfall of 17.54 in. in 1952 which was 5.83 in. below average while 1953 was 5.84 in. below. Both years had a rather severe midseason drought. In 1952 drought started in May and lasted until August only to be followed by two more dry months in September and October. Climate in 1953 was similar except that the midseason drought began one month earlier and the fall dry period lasted one month longer. Although amounts of precipitation during the two seasons were similar, 1952 was a much better year for growth because of high rainfall in 1951 and also because a plentiful supply of moisture was received in March and April of 1952. Temperatures were high during these two low rainfall years averaging 5.5° above normal in June, 1952 and 8.0° above in June, 1953.

TOPOGRAPHY, GEOLOGY, AND SOILS

Much of the nearly level land near Atwood, Kansas has been planted to wheat and other cereals. However, some of the level and much of the rolling land is in grassland and used for livestock production. These grasslands are representative of about 2.5 million acres in Kansas (Fly 1946).

Topography in grasslands generally was quite rough with numerous "cat steps" along gentle slopes. In many places, however, there were exposures of Tertiary rock (Ogallala) along the lower slopes where descent was abrupt into the lowlands.

Soils were mostly loess except along streams and on bedrock along the breaks. Texture was usually fine sandy loam.

The A horizon, especially the first 11-in. section, was very granular in structure and dark in color. Below this to a depth of 23 in. was a gradation in both color and structure. First evidence of columnar structure was at 23 in. Soil was light tan, almost cream colored and only slightly columnar. At 40 in., it was very firm and lacked structure much like a C horizon, yet throughout were signs of deposition which may have been caused by animal burrows and remains of old roots. The soil continued this way throughout to 11 ft where it became more compact. At 15 ft it was quite firm and still contained roots of plants such as skeleton weed (*Lygodesmia juncea*) and false boneset (*Kuhnia eupatorioides*).

At Ashland, Kansas most of the best level land has been cultivated for many years leaving vegetation on the gently rolling to rough topography for grazing of livestock. The areas studied were often nearly level on uplands that slope gradually to lowlands below. In some places, however, slopes were quite steep. Tops of hills were often capped with rock fragments

of Comanchean series, below which was a layer of Permian Red Beds.

Soils were mostly of the Permian Red Beds Soil Province which extends northward 20-30 mi. into Kansas from the south and for a distance of 130 mi. east and west from Caldwell to Ashland (Moore 1931). The same general type of soil is found southward across Central Oklahoma (Bruner 1931). This represents a vast area of several million acres in Kansas and many more in Oklahoma.

Soils in this area were typically sandy loam of various shades of red. Depth, however, varied greatly. In some places rocks occurred near the surface while in others red soil, often with rock fragments of various sizes, was from 5-8 ft in depth.

Horizons in this Permian soil were very difficult to distinguish especially when dry. Soil was mostly granular in the upper 6 in. Color here could be described as chocolate brown with the parent material being masked by organic matter. At a depth of 12 to 18 in., color changed but little with only slightly more of a red cast. Even as deep as 3 ft effect of organic matter was much more pronounced than in soils of limestone derivation. It was apparent that much of this unusual distribution of organic matter was due to activities of earthworms and rodents.

Lines of vertical cleavage began about 6 in. below the surface and extended to 3 ft with many lines going as deep as 4 ft. These breaks were 4 to 8 in. apart and often extended to their full depth without horizontal cleavage. Thus the B horizon began and ended so gradually that it was largely transitional. Its structure could hardly be described as columnar in that the columns were so much larger than usual. With care in removing a column at primary cleavages it was often found to be 6 in. in diameter and 30 in. or more long.

Magnesium and calcium carbonates or other concentrations were difficult to discern. They may not occur in noticeable quantities due to possible shortage of these elements in parent material.

NATIVE VEGETATION

The name "mixed prairie" has been used because this vast plant association is generally composed of a mixture of short, mid and tall grasses. On some areas these different grasses grow in mixed stands while in other areas alternates of nearly pure short grasses and nearly pure mid grasses are found. Percentages of tall, mid and short grasses found in any one community vary with differences in soil, degree of slope, direction of slope, and many other environmental factors. Large areas of pure short grass are found on the more level hardlands of western Kansas while nearby sites with shallow, rocky soils support mixed stands of short, mid and tall grasses.

STUDIES AT ATWOOD

COVER AND COMPOSITION OF GRASSES

Vegetation on deep loessial soils near Atwood is dominated by short grasses on the upland, short and

mid grasses on the gentle hillsides, and tall grasses in the lowland.

The principal grass on the ungrazed upland was blue grama (*Bouteloua gracilis*) which, along with buffalo grass (*Buchloe dactyloides*), formed the understory. The upperstory was composed of side-oats grama (*Bouteloua curtipendula*), big bluestem (*Andropogon gerardi*), little bluestem (*A. scoparius*), red three-awn (*Aristida longisetia*), purple three-awn (*A. purpurea*), western wheatgrass (*Agropyron smithii*), and sand dropseed (*Sporobolus cryptandrus*). Basal cover of vegetation averaged only 28.6% but the interspaces between grasses were filled with a heavy mulch to a depth of 2 in. or more. The two short grasses comprised 60% of the cover (Table 1). Side-oats grama, big bluestem, little bluestem and western wheatgrass were found as isolated bunches growing in slight depressions or other favorable areas. In addition, red three-awn, purple three-awn and sand dropseed were scattered through the short grasses.

TABLE 1. Percentage composition and basal cover of principal grasses on different sites of an ungrazed prairie near Atwood, Kansas.

Species	PERCENTAGE COMPOSITION			
	Upland	Hillside	Sharp break	Lowland
Buffalo grass.....	16.0	9.6	1.1
Blue grama.....	43.4	18.2	0.7
Side-oats grama.....	15.3	44.4	39.5	33.6
Western wheatgrass.....	2.4	1.8	11.2
Big bluestem.....	8.2	2.8	4.5	35.4
Little bluestem.....	6.2	13.9	53.9	13.9
Red three-awn.....	5.8	6.4	0.6
Purple three-awn.....	1.6	1.9
Sand dropseed.....	0.4	0.5	0.9
Canada wild rye.....	1.8
Switch grass.....	0.4
Hairy grama.....	0.3	2.1
Other species.....	0.7	0.2	0.4
Total.....	100.0	100.0	100.0	100.0
Basal cover.....	28.6	27.7	13.8	17.1

Basal cover averaged 27.7% on the hillside with large areas of almost pure side-oats grama especially on the upper slope (Fig. 1). Here also were small patches of little bluestem and blue grama, but on the less abrupt lower slopes both species increased considerably. Over the entire slope, side-oats grama comprised 44.4% of the cover, blue grama 18.2 and little bluestem 13.9%, respectively (Table 1). Buffalo grass occurred in small areas but three-awn grasses were scattered throughout the slope. Big bluestem grew in pure stands forming small clumps, many of which were apparently suffering from the accumulation of too much mulch. Many areas 2 ft in diameter were covered with mulch 4 to 8 in. deep which had retarded production of tillers. Western wheatgrass was found only in small communities at the heads of side ravines (Fig. 1).



FIG. 1. Non-grazed hillside (left) at Atwood. Bunches of little bluestem interspersed among cover of side-oats grama and blue grama. Head of small ravine (right) in ungrazed Atwood prairie. Big bluestem (light color) in center of ravine and western wheatgrass (dark color) around top of ravine.

Open cover of only 13.8% on sharp breaks at the base of hillsides was characterized by the presence of three grasses generally found on abrupt slopes in this part of the Great Plains. Two of these species, little bluestem 53.9%, and side-oats grama 39.5%, made up the bulk of the vegetation. But big bluestem was found in small amounts with 4.5% at the lower part of the breaks.

The lowland was dominated by big bluestem and side-oats grama which together made up 69% of the cover. With western wheatgrass and little bluestem they comprised nearly 95% of the plant cover. They occurred mostly as pure stands with some mixing of side-oats grama and western wheatgrass. Widely scattered short grass plants were found in the understory of western wheatgrass communities. The low basal cover of 17.1% was probably due to excessive mulch. It covered the soil to a depth of more than 12 in. in some places and had an average weight of over 12 tons per acre. Some areas of the lowland were damaged by soil washed in from nearby cultivated fields which allowed invasion by weeds such as common sunflower (*Helianthus annuus*), lamb's quarter (*Chenopodium album*) and tansy mustard (*Descurainia pinnata*). In other areas with only light disturbance Canada wildrye (*Elymus canadensis*) and sand dropseed were quite common.

FORBS

Although the dominant plants of the ungrazed prairie were grasses, forbs were quite abundant and formed a conspicuous part of the vegetation. For example, salmon colored mallow (*Sphaeralcea coccinea*) was found to average 9 plants per 100 sq ft on the upland (Table 2).

This forb has been described as being very resistant

TABLE 2. Distribution of forbs on the 3 sites of non-grazed prairie near Atwood. Relative abundance of most prevalent forbs on certain sites is given. Occurrence of less abundant ones is indicated (X). Figures show number of plants per 100 sq ft.

Name of forb	Upland	Hillside	Lowland
<i>Acerates viridiflora</i>	x	..
<i>Ambrosia psilostachya</i>	2.3
<i>Artemisia dracunculoides</i>	1.1	7.2	..
<i>Artemisia frigida</i>	x	x	..
<i>Asclepias pumila</i>	6.8	4.7	..
<i>Aster ericoides</i>	5.0	2.8	1.3
<i>Aster oblongifolius</i>	x	4.7	4.9
<i>Astragalus gracilis</i>	x	x	..
<i>Astragalus lotiflorus</i>	x
<i>Astragalus missouriensis</i>	x	x	..
<i>Astragalus mollissimus</i>	x
<i>Castilleja sessiliflora</i>	x
<i>Cirsium undulatum</i>	3.5	x	0.6
<i>Conyza canadensis</i>	x
<i>Dalea enneandra</i>	x	x	..
<i>Erysimum asperum</i>	x	x	..
<i>Gaura coccinea</i>	1.0	x	x
<i>Glycyrrhiza lepidota</i>	1.3
<i>Gutierrezia sarothrae</i>	x	x	..
<i>Haplopappus spinulosus</i>	y	y	..
<i>Kuhnia eupatorioides</i>	x	x	x
<i>Liatris punctata</i>	x	1.5	x
<i>Linum compactum</i>	x	..
<i>Linum rigidum</i>	x	x	..
<i>Lithospermum incisum</i>	x	x	..
<i>Lygodesmia juncea</i>	3.0	3.6	1.9
<i>Oenothera serrulata</i>	1.4	2.8
<i>Opuntia macrorrhiza</i>	x	x	..
<i>Oxytropis lambertii</i>	x	x	..
<i>Pentstemon albidus</i>	x	x
<i>Petalostemon candidum</i>	y
<i>Physalis</i> spp.....	x
<i>Polygala alba</i>	x	x	..
<i>Prunus</i> spp.....	x
<i>Psoralea argophylla</i>	1.0	6.3
<i>Psoralea esculenta</i>	x	x
<i>Psoralea tenuiflora</i>	2.8	1.2	x
<i>Ratibida columnifera</i>	x	x	..
<i>Senecio platensis</i>	x
<i>Schrankia nuttalli</i>	x	..
<i>Solidago missouriensis</i>	x	4.7	4.9
<i>Solidago mollis</i>	x	x	8.3
<i>Sphaeralcea coccinea</i>	9.0	x	2.5
<i>Symphoricarpos</i> spp.....	x
<i>Thelesperma megacarpum</i>	y	..
<i>Verbena bracteosa</i>	x
<i>Verbena stricta</i>	x	x
<i>Yucca glauca</i>	x	y	..

to both drought and heavy grazing (Weaver & Albertson 1943).

The 5 most common forbs on the upland were salmon colored mallow, plains milkweed (*Asclepias pumila*), many flowered aster (*Aster ericoides*), wavy leafed thistle (*Cirsium undulatum*), and skeleton weed (*Lygodesmia juncea*) in that order of abundance. On the hillsides the 5 most common were green sagewort (*Artemisia dracunculoides*), Missouri goldenrod (*Solidago missouriensis*), plains milkweed, oblong-leaved aster (*Aster oblongifolius*) and skeleton weed. The most abundant on the lowland site were plains goldenrod (*Solidago mollis*), silver leaf scurf-pea (*Psoralea argophylla*), Missouri goldenrod, ob-

long-leaf aster and serrate-leaved evening primrose (*Oenothera serrulata*). Several species of forbs were found on all 3 sites.

There were 48 species of forbs recorded for the entire area and probably some of the less abundant ones were not recorded. Seventeen families were represented of which the most common were Compositae and Leguminosae.

FORAGE PRODUCTION

Yields were considerably higher in 1952 than in 1953. Production in 1952 was 3,274 lbs/A on the lowland, 2,463 lbs on the upland, and 1,902 lbs on the hillside (Fig 2). From 70 to 78% of the forage was produced during the first half of the growing season. Yields prior to June 1 for the three sites were 1,124 lbs/A on the lowland, 773 lbs on the hillside and 739 lbs on the upland. A definite increase in forage for the lowland (1,426 lbs) and upland (999 lbs) was harvested in June but yield on the hillside decreased slightly. July yields decreased slightly on all sites and less than 4% of the total yield was harvested in August. The more mesic lowlands maintained more continuous growth than either of the other two locations.

Yield in 1953 was only 1,911 lbs/A on the lowland, 1,384 lbs on the upland, and 1,239 lbs on the hillside. From 80 to 97% of the forage was produced during the first half of the growing season. This is a considerably greater percentage than was harvested during May and June in 1952 and probably was due to a tremendous reduction in the June yield of 1953. Production before the first of June was 1,081 lbs on the lowland, 998 lbs on the upland, and 716 lbs on the hillside. Lack of subsoil moisture at the beginning of the growing season in 1953 is reflected in the sharp reductions in June yield. While production increased from May to June in 1952 it decreased in June of 1953 to 439 lbs on the lowland, 355 lbs on the upland and 449 lbs on the hillside. The relatively good production of 376 lbs on the lowland in July compared to 19 lbs on the upland and 62 lbs on the hillside shows clearly the more mesic nature of the lowland. Yields in August were again negligible at all locations.

ROOT STUDIES

Deep loessial soils at Atwood were favorable to deep penetration of the roots of prairie plants. Working in the same soil type, Weaver & Bruner (1948) found that grasses and forbs had well-branched, deeply penetrating roots. Hopkins (1951) found most of the important grasses and forbs in the loess hills of Nebraska had root systems of 6 to 20 ft. Root systems of ungrazed plants at Atwood varied from 4 ft to more than 18 ft in depth (Fig. 3).

Skeleton weed produced a single tap root, with relatively few branches, that penetrated this permeable soil to more than 18 ft. Other forbs such as rayless thelesperma (*Thelesperma megapotamicum*), salmon colored mallow, scarlet gaura, serrate-leaved

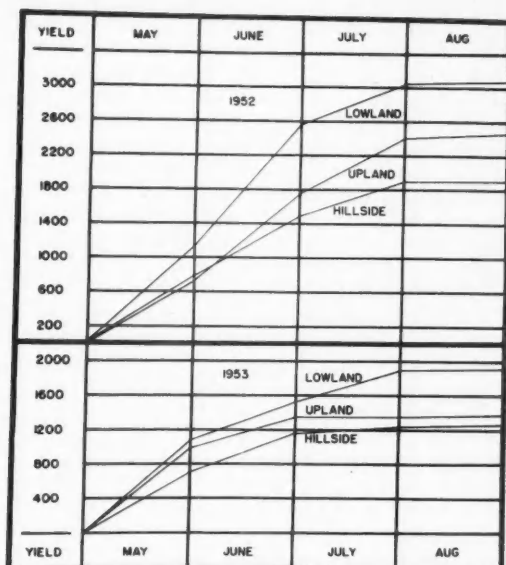


FIG. 2. Cumulative monthly yields of forage in pounds per acre on the nongrazed prairie at Atwood, Kansas for 1952 and 1953.

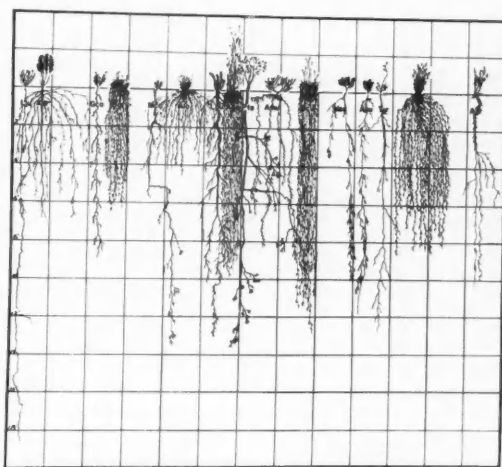


FIG. 3. Depth and lateral spread of roots of principal species of grasses and forbs on nongrazed prairie at Atwood, Kansas. From left to right are: *Lygodesmia juncea* (Lju), *Artemisia dracunculoides* (Adr), *Gaura coccinea* (Geo), *Bouteloua gracilis* (Bgr), *Sphaeralcea coccinea* (Meo), *Aristida longiseta* (Alo), *Liatris punctata* (Lpu), *Andropogon gerardi* (Age), *Psoralea tenuiflora* (Pte), *Aster ericoides* (Amu), *Bouteloua curtipendula* (Bcu), *Oenothera serrulata* (Mse), *Asclepias pumila* (Apu), *Thelesperma megapotamicum* (Tgr), *Andropogon scoparius* (Asc), *Astragalus gracilis* (Agr).

evening primrose, and plains milkweed had long slender tap roots (9 to 14 ft in depth) with but few short laterals. Tap roots of wild alfalfa, blazing star (*Liatris punctata*) and slender loco (*Astragalus gra-*

cilis) were very large especially in the upper few feet of soil. Large lateral branches were well spaced along the main root. Roots of these plants were found to be as much as .05 to 1 in. in diameter near the surface of the soil and ranged in depth from 10 to 14 ft. The root system of green sage extended only to 7 ft but it was characterized by many strong branches arising near the surface of the soil giving it a lateral spread of 2 to 3 ft. Many flowered aster had well developed rhizomes, and long roots extended downward from these underground stems. The excavated plants of this species seemed to possess only those roots extending downward from its rhizomes.

Roots of grasses varied in depth of penetration from 4 to 12 ft. Red three-awn had a very shallow root system but the roots extended laterally nearly 2 ft from the center of the plant. On the other hand, roots of blue grama, big bluestem and side-oats grama grew almost straight down from the tops to depths of 7 to 13 ft but did not extend laterally any farther than the parts above ground. Generally the roots of blue grama were finer and more dense than those of big bluestem and side-oats grama. The root system of little bluestem penetrated deeply (9 ft) and also had a lateral spread of nearly 3 ft.

STUDIES AT ASHLAND

COVER AND COMPOSITION OF GRASSES

The shallow red soils at Ashland supported more midgrasses than the deep loessial soils at Atwood. On the uplands only about 27% of the vegetation was short grasses while at Atwood they comprised 60% of the total.

On areas dominated by short grasses, basal cover was often as high as 50 to 75% while on other areas with mostly bunch grasses such as red three-awn, cover was as low as 8%. Most of the areas sampled had a basal cover ranging from 20 to 40% and the average for the entire site was 32.1 (Table 3). Side-oats grama alone comprised 40% of the vegetation and little blue-stem and the three-awn grasses together made up 23.4% of the cover. The three principal short grasses were blue grama, hairy grama (*Bouteloua hirsuta*) and buffalo grass in order of abundance.

Open cover on hillsides of only 22.2% was dominated by two midgrasses, little bluestem and side-oats grama, while hairy grama was the most important short grass (Fig. 4). Although they were not plentiful anywhere on the slope, the 3 short grasses occurred most abundantly on the upper slopes and on the more level lower slopes. Small bunches of red three-awn were also scattered among the other grasses.

Hairy grama comprised 23.5% of the vegetation on the sharp breaks and thus helped provide greater basal cover (20.2%) than usual for this site. The other 2 dominant grasses here were little bluestem, 35.2% and side-oats grama, 31.4%. Moderate amounts of big bluestem were found but other grasses were very minor in importance.

TABLE 3. Percentage composition and basal cover of principal species of grass on different sites on an ungrazed prairie near Ashland, Kansas.

Species	PERCENTAGE COMPOSITION			
	Upland	Hillside	Sharp break	Lowland
Buffalo grass.....	4.9	2.0	0.3
Blue grama.....	16.8	5.5	0.9	5.3
Side-oats grama.....	50.0	37.8	31.4	18.6
Big bluestem.....	0.9	7.8	50.9
Little bluestem.....	14.9	40.0	35.2	8.2
Hairy grama.....	4.9	9.7	23.5	2.7
Sand dropseed.....	0.9
Red three-awn.....	1.3	2.1	0.2
Purple three-awn.....	7.2	0.9	0.1	0.6
Silver beardgrass.....	0.1	1.6
Sedges.....	2.4
Tall dropseed.....	4.5
Indian grass.....	3.5
Switch grass.....	1.0	1.2
Other species.....	0.2
Total.....	100.0	100.0	100.0	100.0
Basal cover.....	32.1	22.2	20.2	16.2



FIG. 4. East facing gentle slope on relict prairie at Ashland, Kansas. Grasses are side-oats grama, little bluestem, hairy grama, blue grama, and purple three-awn.

The heavy mulch and dominance of rhizomatous grasses were at least partly responsible for the relatively open cover of 16.2% on the lowlands. Many grasses were found on this site but big bluestem made up over half the plant cover and was found most extensively in the bottoms of the ravines. Moderate amounts of side-oats grama, blue grama and little bluestem were found especially on the upper fringes

of the lowland. Minor grasses recorded here were hairy grama, silver beardgrass (*Andropogon saccharoides*), switch grass (*Panicum virgatum*), purple three-awn and buffalo grass. Heavy sedge (*Carex gravida*) was found in small bunches on moist portions of this site.

FORBS

Forbs were also quite plentiful at Ashland with 45 species recorded in the samplings and observations. The 5 most abundant forbs on the upland were blazing star (*Liatris punctata*), wild alfalfa (*Psoralea tenuiflora*), snakeroot (*Echinacea angustifolia*), hairy goldaster (*Chrysopsis villosa*) and serrate-leaved evening primrose (Table 4). On the hillside the five most common were western ragweed (*Ambrosia psilostachya*), many flowered aster, wild alfalfa, broom snakeweed (*Gutierrezia sarothrae*) and tall evening primrose (*Stenosiphon linifolius*). The most abundant on the lowland were western ragweed, plains goldenrod, many flowered aster, purple poppy mallow (*Callirhoe involucrata*) and ironweed (*Vernonia baldwini*).

Fifteen different families were represented by the forb population. The most common families were Compositae, Leguminosae and Onagraceae.

FORAGE PRODUCTION

Production in 1952 was 3,364 lbs/A on the lowland, 1,225 lbs on the hillside and 1,175 lbs on the upland (Fig. 5). From 82 to 85% of the forage was produced on the hillside and upland, respectively, during the first half of the growing season but during the same period the lowland produced only 59% of the seasonal yield. Production prior to June 1 was 726 lbs on the lowland, 605 lbs on the hillside and

TABLE 4. Distribution of forbs on the 3 sites of non-grazed prairie near Ashland. Relative abundance of most prevalent forbs on certain sites is given. Occurrence of less abundant ones is indicated (X). Figures indicate number of plants per 100 sq. ft.

Name of forb	Upland	Hillside	Lowland
<i>Ambrosia psilostachya</i>	1.0	8.3	15.8
<i>Antennaria neglecta</i>	x
<i>Asclepias engelmanniana</i>	x
<i>Asclepias verticillata</i>	x	..
<i>Aster arenosus</i>	x
<i>Aster ericoides</i>	x	5.2	4.8
<i>Aster oblongifolius</i>	x	..
<i>Callirhoe involucrata</i>	1.4
<i>Castilleja citrina</i>	x
<i>Chamaesaracha conoides</i>	x
<i>Chrysopsis villosa</i>	2.0
<i>Cirsium undulatum</i>	x	x	x
<i>Croton texensis</i>	x	..
<i>Dalea aurea</i>	x
<i>Desmanthus illinoensis</i>	x
<i>Echinacea angustifolia</i>	2.3	x	x
<i>Engelmannia pinnatifida</i>	x	..
<i>Erigeron strigosus</i>	x	..
<i>Gaura coccinea</i>	x
<i>Gutierrezia dracunculoides</i>	x
<i>Gutierrezia sarothrae</i>	1.9	1.7	x
<i>Haplopappus spinulosus</i>	x	x	x
<i>Hoffmanseggia jamesii</i>	x	x
<i>Houstonia nigricans</i>	x
<i>Hymenozys acaulis</i>	x
<i>Hymenozys scaposa</i>	x	x	..
<i>Kuhnia eupatorioides</i>	x	x
<i>Lesquerella ovalifolia</i>	x
<i>Liatris punctata</i>	3.2	..	x
<i>Linum rigidum</i>	x	..
<i>Melampodium cinereum</i>
<i>Mirabilis linearis</i>	x	..
<i>Oenothera lavandulaefolia</i>	x	x	..
<i>Oenothera serrulata</i>	1.9	x	..
<i>Opuntia macrorrhiza</i>	x	x	..
<i>Penstemon albidus</i>	x	..
<i>Psoralea lanceolata</i>	1.3
<i>Psoralea tenuiflora</i>	2.8	2.8	x
<i>Ratibida columnifera</i>	x	x	..
<i>Sphaeralcea coccinea</i>	x	x	1.0
<i>Salvia pitcheri</i>	x
<i>Schrankia nuttalli</i>	x	x	x
<i>Scidage mollis</i>	x	10.4
<i>Stenosiphon linifolius</i>	x	x	1.2
<i>Thelesperma megapotamicum</i> ...	x	x	1.1
<i>Vernonia baldwini</i>	1.3
<i>Yucca glauca</i>	x	..	x

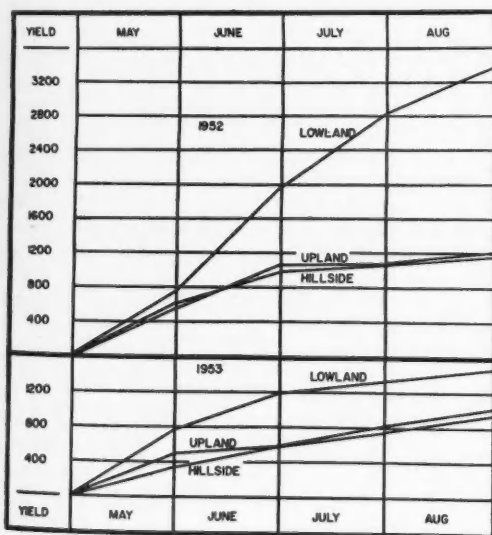


Fig. 5. Cumulative monthly yields of forage in lbs/A on the nongrazed prairie at Ashland, Kansas.

585 lbs on the upland. The average monthly yield on lowland was 1,262 lbs in June but only 375 lbs on the hillside and 403 lbs on the upland. Production on the hillside and upland in July was very low, due to low rainfall during the previous month. However, the more mesic lowland produced 854 lbs during this month. Above average precipitation in August seemed to stimulate renewed growth on all sites and yields for this month were 522 lbs on the lowland, 164 on the hillside and 146 on the upland.

Yields in 1953 were 1,490 lbs/A on the lowland, 1,020 on the upland, and 1004 lbs on the hillside (Fig. 5). Rainfall during spring and early summer was extremely low during both years but high rainfall in April, 1952 apparently made that season more

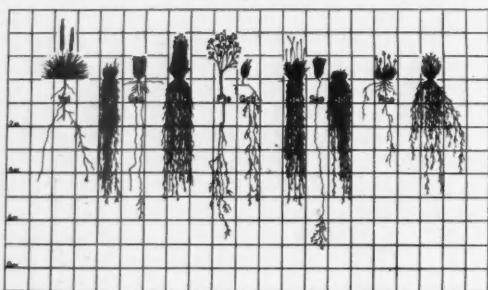


FIG. 6. Depth and lateral spread of roots of principal species of grasses and forbs on nongrazed prairie at Ashland, Kansas. From left to right are: *Yucca glauca* (Ygl), *Bouteloua gracilis* (Bgr), *Gutierrezia sarothrae* (Gsa), *Andropogon scoparius* (Asc), *Psoralea tenuiflora* (Pte), *Gaura coccinea* (Geo), *Bouteloua curtipendula* (Bcu), *Haplopappus spinulosus* (Ssp), *Buchloe dactyloides* (Bda), *Ratibida columnifera* (Rco), and *Aristida longiseta* (Alo).

favorable for early growth. For example, in 1953 only 56 and 57% of the yield was produced prior to July 1 on the upland and hillside, respectively. Prior to June 1 production was 782 lbs/A on the lowland, 476 lbs on the upland and 385 lbs on the hillside. Except for the lowland, yields were quite low in June but increased again in July and August.

ROOT STUDIES

Roots of plants at Ashland did not penetrate the soil as deeply as similar plants did at Atwood (Fig. 6). The tighter soil underlain by rock 5 or 6 ft below the surface limited their growth. Maximum depth of the principal grasses was seldom more than 5 ft, but all grasses studied had roots at that depth.

Roots of three-awns had a much wider lateral spread than did the other grasses but had less roots in the deeper layers of the soil. Maximum depth of forb roots was also limited to 7 ft or less because of the character of the soil. The long tap roots of these forbs contained very few branches until they reached below 5 ft where a very tight clay soil occurred between the rocks and there many branch roots were found.

EFFECT OF GRAZING

PERCENT COMPOSITION AND COVER

Grazing in these two areas of the mixed prairie caused a decrease in mid and tall grasses and a proportionate increase in short grasses. On the more xeric uplands at Atwood 40% of the cover of ungrazed prairie was formed by mid and tall grasses but this amount was reduced to 22% under moderate use and to only 5% when heavily grazed. Loss of mid and tall grasses on the heavily stocked pasture was equally pronounced on the hillsides but the taller grasses sustained themselves fairly well under moderate use. Here large patches of side-oats grama and little bluestem, 6 to 20 ft across, formed alternates with areas of blue grama of almost equal size. Low-

lands were always the most heavily utilized sites in this area. For example, lowland in a moderately grazed pasture was generally heavily utilized. Reduction of the more palatable species like big bluestem, side-oats grama and little bluestem was quite marked in lowlands of the moderately grazed pasture and they had almost disappeared in the heavily used area.

At Ashland grazing had the same general effects on the vegetation as at Atwood. Mid and tall grasses were reduced under moderate use and were almost eliminated under heavy grazing. In fact, cover of short grasses on heavily used lowlands had broken and allowed invasion of annual weeds.

Response of grasses to grazing has become useful in measuring condition of many livestock ranges. It has been found that some native grasses, when grazed, decrease in abundance while some increase. If grazing pressures become too severe, weedy plants invade from the outside (Weaver & Hansen 1941). Grasses found on the two areas of this study were very responsive to grazing pressures. Dyksterhuis (1949) has labelled these plants as decreasers, increasers and invaders.

Buffalo grass proved to be the most conspicuous increaser of all the grasses. On the uplands it increased from 16% on nongrazed to nearly 91% on heavily grazed areas at Atwood and from less than 5 to 90% under the same treatments at Ashland (Figs. 7 & 8). This low growing species increased tremendously on all sites under moderate grazing as well as with heavy use. On the Atwood lowlands where it comprised only one percent or less of the climax vegetation, it became the most common grass on heavily grazed areas. This tendency of buffalo grass to increase rapidly with grazing is made possible by its low growing point and the rapid growth of its stolons: Branson (1953) found that most increasers had low growing points and that the growing point of buffalo grass was never found above the surface of the soil. The stolons of this grass have been observed to grow as much as 5 cm a day under optimum conditions (Webb 1941). However, in another study under normal field conditions, they averaged about 20 cm during the growing season (Tomanek 1948). Rapid growth of buffalo grass stolons has made this species valuable in providing quick cover on areas denuded by drought, dusting or overuse. Although a large percentage composition of buffalo grass is generally indicative of overutilization, it is still a very valuable grass in these areas. It is relished by cattle and preserves more of its nutrients in the winter than most of the taller grasses.

Blue grama is usually classed as an increaser. It increased with moderate grazing but decreased with heavy use on all sites at Ashland. However, it also decreased with moderate grazing on the upland at Atwood. Although it is fairly resistant to grazing it has difficulty competing with buffalo grass in occupying soil abandoned by decreasers.

Side-oats grama was a decreaser on some sites but

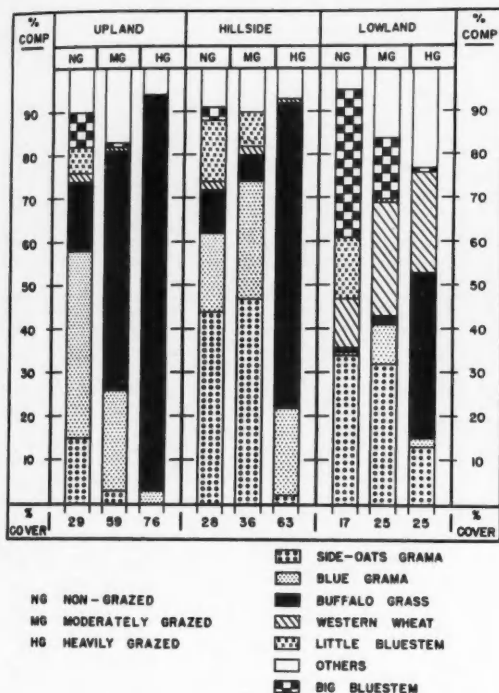


FIG. 7. Changes in composition of the vegetation on three sites due to different intensities of grazing at Atwood, Kansas.

increased on others. On the more xeric uplands it decreased very rapidly. However, on the hillsides and lowlands it became slightly more abundant with moderate grazing but decreased with heavy use.

The presence of little bluestem is often used as an indicator of light or nongrazing because of its rapid decrease with moderate and heavy use. It was a conspicuous part of the vegetation on all ungrazed sites of both study areas but either disappeared or decreased greatly with grazing. It was not found on any of the heavily grazed locations.

Big bluestem is also a decreaser but seems to be somewhat more resistant to grazing than little bluestem. It was most common on the lowlands where it was found to decrease from 50% of the cover on the nongrazed area at Ashland to less than 2% on the heavily grazed site. The reaction was very much the same at Atwood where it was also found on the hillside and upland sites.

Western wheatgrass is the only important cool season grass in this area. It is generally found on lowland sites or on locally heavy soils of the upland and hillside. On lowland, where it was most common, it increased with moderate grazing but gave way to the short grasses with heavy use. It generally decreased on the upland and hillside.

Hairy grama increased on the upland at Ashland

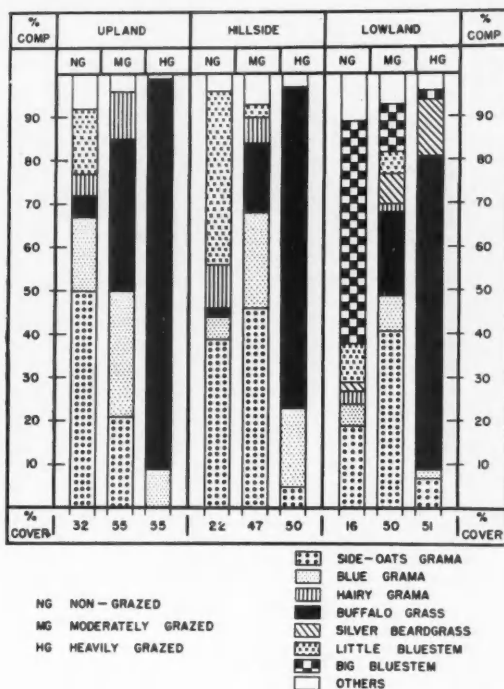


FIG. 8. Changes in composition of vegetation on three sites at Ashland, Kansas due to different intensities of grazing.

but decreased on the hillside and lowland. It was not found in measurable quantities at Atwood.

Several other grasses occurred at these two study areas. Many of them were invaders which became more plentiful with moderate grazing. However, some of these invaders are quite palatable and not very aggressive and, therefore, were not as abundant under heavy grazing. Even though some of them may be palatable, their instability makes them undesirable.

Reaction of these important grasses provides a group of indicators for measuring the degree of grazing to which an area has been subjected.

Reaction of forbs was not thoroughly studied. Although forb counts were made in this study on areas with different degrees of grazing they were not extensive enough to enable the investigators to classify all the plants found. Some forbs, however, were sufficiently plentiful to be accurately classified. Five of the most common decreasers were *Psoralea tenuiflora*, *Aster ericoides*, *Solidago missouriensis*, *Liatris punctata*, and *Echinacea angustifolia*. Increasers were *Sphaeralcea coccinea*, *Ratibida columnifera*, *Gutierrezia sarothrae*, *Aster arenosus*, and a shrub, *Symphoricarpos occidentalis*. Common plants invading disturbed areas were *Euphorbia marginata*, *Solanum rostratum*, *Helianthus annuus*, *Kochia scoparia* and *Lactuca ludoviciana*.

FORAGE PRODUCTION

Forage production was generally reduced by grazing and the greatest reduction occurred under heavy use. Yields in 1952 on heavily grazed sites at Atwood were less than half those collected on similar sites at the nongrazed location (Table 5). Heavy use on upland reduced the yield from 2,463 lbs/A (on the nongrazed) to 1,173 lbs. Similarly, the nongrazed area produced 1,902 lbs/A on the hillside and 3,274 lbs on the lowland while yields on heavily used

TABLE 5. Seasonal yields of forage on 3 sites of non-grazed (NG), moderately-grazed (MG) and heavily-grazed (HG) pastures near Atwood, Kansas during growing seasons of 1952 and 1953.

	1952			1953		
	NG	MG	HG	NG	MG	HG
UPLAND.....	2463	1920	1173	1384	665	430
Mid grass.....	1085	354	11	197	87	420
Short grass.....	1084	1124	980	868	553	420
Forbs.....	294	442	182	319	24	10
HILLSIDE.....	1902	2043	1031	1239	800	408
Mid grass.....	1524	1431	326	934	536	5
Short grass.....	194	355	547	117	121	427
Forbs.....	181	257	158	188	143	48
LOWLAND.....	3274	2425	1482	1911	1213	1319
Mid grass.....	3169	1836	819	1770	969	650
Short grass.....	18	375	471	27	132	167
Forbs.....	87	214	192	114	62	502

sites were only 1,031 and 1,482 lbs respectively. In comparison to ungrazed yield as given above, moderate use reduced production on the upland and lowland to 1,920 and 2,425 lbs respectively, but increased on the hillside to 2,043 lbs.

At Ashland yield on the nongrazed upland was 1,175 lbs/A in 1952 with nearly 800 lbs produced by mid grasses and 200 lbs by the 2 short grasses (Table 6.) Although short grasses made up 36% of the cover they only produced about 20% of the grass yield. Under moderate use production increased 537 lbs over nongrazing, making a yield of 1,712 lbs/A. Only 971 lbs/A were harvested on this site under heavy use. Production on the moderately grazed hillside, as at Atwood, was more than on the nongrazed site. As mentioned earlier, when large quantities of mulch collect as the result of nongrazing the basal cover is greatly reduced which might also result in a decreased yield.

Heavily grazed hillsides at Ashland produced 1,109 lbs of forage, 20% of which was composed of forbs, most of which were unpalatable to cattle. Moderate grazing reduced yields on the lowland from 3,364 lbs on nongrazed to 2,649; and heavy use reduced it to 2,042 lbs.

As mentioned previously, 1953 was a very poor year for growth of vegetation which resulted in low forage production (Table 5). Areas which had been subjected to heavy grazing suffered most from the

TABLE 6. Seasonal yield of forage on 3 sites of non-grazed (NG), moderately-grazed (MG) and heavily-grazed (HG) pastures near Ashland, Kansas during growing seasons of 1952 and 1953.

	1952			1953		
	NG	MG	HG	NG	MG	HG
UPLAND.....	1175	1712	971	1020	927	731
Mid grass.....	791	180	27	764	503	10
Short grass.....	200	1150	893	149	390	712
Forbs.....	184	382	115	107	34	9
HILLSIDE.....	1225	1536	1109	1004	1300	590
Mid grass.....	868	762	134	843	589	15
Short grass.....	229	557	763	52	671	567
Forbs.....	128	217	212	109	40	8
LOWLAND.....	3364	2649	2042	1490	1160	1038
Mid grass.....	2724	2122	595	754	836	146
Short grass.....	48	162	1035	148	889
Forbs.....	592	365	142	736	175	3

drought. Production at Atwood under heavy use was only 430 lbs on the upland and 408 lbs on the hillside which represents a reduction of 63 and 53% respectively, from the 1952 yields. A yield of 1,319 lbs. was harvested on the heavily grazed lowland in 1953, 37% of which was furnished by weedy forbs. Poor growing conditions also greatly affected yields in the moderately grazed pasture. Only 665 lbs of forage were harvested on the upland, 800 lbs on the hillside and 1,213 lbs on the lowland.

There was very little difference in the amount of forage produced on the nongrazed and moderately grazed pastures at Ashland in 1953 (Table 6). All yields were considerably lower than they were in 1952. Production on the moderately grazed upland was 927 lbs/A, on the hillside it was 1,300 lbs and 1,160 on the lowland. A total yield of 731 lbs was harvested on the heavily grazed upland, 590 lbs on the hillside and 1,038 lbs on the lowland. A 5 in. local rain was received at this location and not at the moderately and unused ranges. Even with this additional moisture, yields were below the level of production in the other two pastures.

MONTHLY YIELDS PATTERNS

Most forage production in Central Great Plains occurs before July 1 (Albertson, Riegel & Launchbaugh 1953). In another study, production for April, May and June on a moderately grazed upland pasture in Western Kansas comprised 74% of the yield for the entire season (Tomanek 1948).

An examination of monthly yields from the two areas discussed in this study showed some rather interesting variations due to different grazing intensities. Fig. 9 illustrates monthly yields on the upland and hillside sites for both 1952 and 1953. The pattern of forage production was quite different when comparing one year with the other. On both sites in 1952 the moderately grazed location had the highest production before June 1 but decreased rather

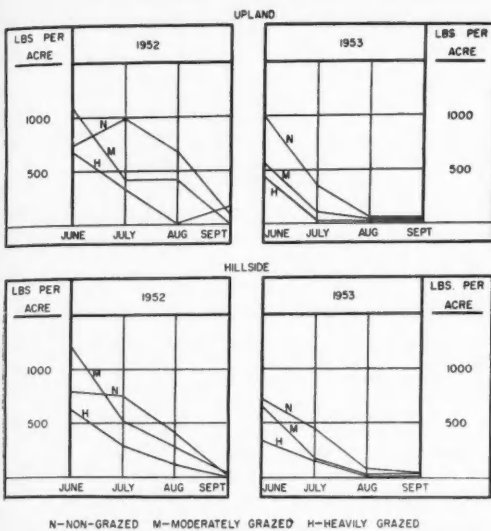


FIG. 9. Monthly yield patterns on upland and hillside site of nongrazed, moderately grazed and heavily grazed pastures at Atwood, Kansas.

steadily thereafter. Although production for the nongrazed and heavily grazed locations was about the same on June 1, yields on the ungrazed increased considerably in June and then gradually decreased. The heavily grazed, on the other hand, decreased rapidly after the first month. The slow start of the ungrazed may have been caused by the insulating effects of the heavy layer of mulch found at that location. As a result the soil became warm enough for growth much later than at other locations. Soil of the heavily grazed area was probably sufficiently warm in May but here the misused plants were too weak for renewed growth, whereas, plants of the moderately used site were more vigorous and the light mulch enabled them to respond earlier to the warming rays of sun. This pattern of monthly production was characteristic of all these sites at both Ashland and Atwood.

The story in 1953, however, was quite different. The nongrazed locations had the highest yield early in the season and decreased steadily thereafter. They yielded more each month than the moderately used areas. Furthermore, yield on the latter areas was greater than on the heavily grazed locations. It is significant that average temperature for March, 1952, was 4° below normal, but for March, 1953, it was 6° above. Warm season grasses generally begin growth about the middle of April. However, the higher temperatures during March, 1953, possibly penetrated the heavy mulch on the nongrazed pasture before growth usually starts and thus eliminated the delaying effect of mulch on early production.

ROOT DEVELOPMENT

Effects of overgrazing are often very apparent in the root systems of abused plants. Grazing fre-

quently results in a reduction in depth and quantity of roots of prairie plants (Weaver 1950; Albertson, Riegel & Launchbaugh 1953). Comparison of root systems excavated at Atwood on nongrazed and heavily grazed (Fig. 10) locations readily show the detrimental effects of overuse. Roots of two heavily grazed forbs (wild alfalfa and salmon colored mallo) extended only half as deeply into the soil and were not as widespread laterally as roots of the same plants on ungrazed areas. The same general differences were found when comparing the grasses. The root system of a heavily grazed red three-awn plant was only 2 ft long and had a lateral spread of less than 2.5 ft whereas roots of the ungrazed plant were 4 ft long and extended laterally over 4 ft. Depth of penetration of roots of heavily grazed and non-grazed blue grama plants was not greatly different but the number of main and branch roots was significantly reduced on the overgrazed plant.

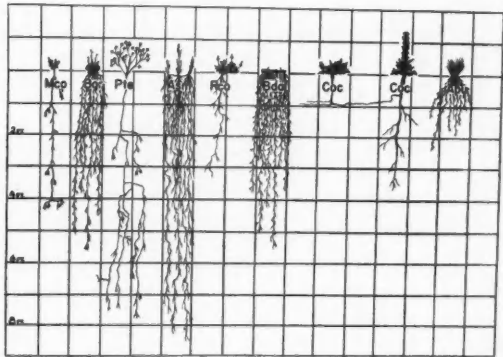


FIG. 10. Depth and lateral spread of roots of principal species of grasses and forbs on heavily grazed prairie at Atwood, Kansas. From left to right are: *Sphaeralcea coccinea* (Meo), *Bouteloua gracilis* (Bgr), *Psoralea tenuiflora* (Pte), *Agropyron smithii* (Asm), *Ratibida columnifera* (Reo), *Buchloe dactyloides* (Bda), *Cirsium ochrocentrum* (Coc), *Aristida purpurea* (Apu).

Effect of grazing on root systems at Ashland was not quite as striking as it was at Atwood (Fig. 11). In fact, roots of heavily grazed plants penetrated slightly deeper than those of nongrazed plants. This was due primarily to the deeper soil above the rock and clay layer on the heavily grazed area which allowed the roots to penetrate more freely than on the shallower soils of the nongrazed location. One difference was apparent, however, between the two areas. The roots of the grasses on the nongrazed area were much more numerous than those of the heavily used areas. Where the roots encountered the rocky clay layer they seemed to branch more profusely than they did at higher levels.

DISCUSSION

The mixed prairie as defined by Clements (1916) consists of a mixture of short grasses and mid grasses. A comparison of the two ungrazed prairies in north-

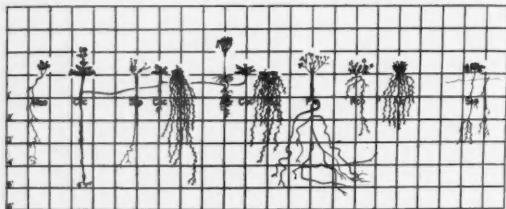


FIG. 11. Depth and lateral spread of roots of principal species of grasses and forbs on heavily grazed prairie at Ashland, Kansas. From left to right are: *Sphaeralcea coccinea* (Meo), *Cirsium ochrocentrum* (Coe), *Haplopappus spinulosus* (Ssp), *Bouteloua gracilis* (Bgr), *Gutierrezia dracunculoides* (Adr), *Buchloe dactyloides* (Bda), *Psoralea tenuiflora* (Pte), *Ratibida columnifera* (Reo), *Aristida longisetia* (Alo), *Sophora sericea* (Sse).

west and southwest Kansas reveal the mixed nature of their plant cover. Both were dominated by a mixture of mid and short grasses and, for the most part, by the same species. However, the proportionate amounts of those species were quite different. Nearly 60% of the cover on the uplands of the loessial soils near Atwood was furnished by short grasses while at Ashland they comprised only 25% of the cover. The principal grass on the uplands at Atwood was blue grama but at Ashland it was side-oats grama.

Short grasses were also more common on the hill-sides of the Atwood prairie but were not important on the sharp breaks and lowlands of either prairie except for hairy grama on the sharp breaks at Ashland. Even though the proportionate amounts of the species varied considerably on the two prairies their similarity is shown by the fact that 85% or more of the grass cover is furnished on every site in both areas by only 6 grasses.

The relatively large amounts of midgrasses on the prairies near Ashland may be due to several environmental factors. The annual precipitation at Ashland averages 23.37 in. while that at Atwood is only 18.53 in. Albertson (1937) found, however, that the short grasses on a prairie near Hays, Kansas furnished fully 80% of the vegetation on the uplands. The average annual precipitation at Hays is 23.05 in. One of the principal factors that might affect the composition on these areas is the difference in soils. The soils of the uplands at Hays are silty clay loams while those at Atwood were fine sandy loams and at Ashland the sandy loam soils contained fragments of rock. The latter soil is probably the most permeable to water and therefore could support a more mesic type of vegetation. Rock fragments in the surface of soils provide entranceways for water to percolate into the soil. Where percolation is slowed, run off is accelerated. Albertson (1937) found that percolation into the rocky soil was over twice as rapid over a 9-hr period as it was in the heavier textured upland soil. The sandy loam soils of Atwood would naturally take water more rapidly than the silty clay loam soils near Hays. Soils are probably not the only factor influencing the variation

in composition on these prairies but they are an important one. Coupland (1950) working in the mixed prairie of Canada found that soil and position on the slope were two very important factors influencing the composition of the vegetation. Three faciations which occur commonly in Canada are Boutelous-Stipa, Stipa-Bouteloua and Stipa-Agropyron. The Bouteloua-Stipa faciation occurs mostly on the more xeric upper slopes of the brown soils while the Stipa-Bouteloua faciation occurs on the mid and lower slopes of the brown soils zone but on the upper slopes of the dark brown soils. The last faciation, Stipa-Agropyron, requires a more mesic habitat and is found principally on the lower slopes of the dark brown soil area. The dominant species of these 3 faciations were needle-and-thread (*Stipa comata*), blue grama, June grass (*Koeleria cristata*), western wheatgrass (*Agropyron smithii*), thickspike wheatgrass (*A. dasystachyum*), needle leaved sedge, (*Carex eleocharis*) and shortawn porcupinegrass (*Stipa sparsata* var. *curtiseta*).

Southward through the mixed prairie the species change somewhat but the relationship of short and mid grasses is quite similar. Hanson & Whitman (1938) found that one of the principal faciations in North Dakota was quite similar to Canada. It was dominated by blue grama, needle-and-thread, *Carex* spp., western wheatgrass, and June grass. However, they found little bluestem to be dominant on steep north-facing slopes. Wright & Wright (1948) worked on a small butte near Billings, Montana and found the dominants to be blue grama, thread-leaved sedge (*Carex filifolia*), needle-and-thread and blue bunch wheatgrass (*Agropyron spicatum*). The dominants in South Dakota were essentially the same, especially on deeper soils (Albertson & Tomanek 1954). However, on shallower soil containing rock fragments side-oats grama and little bluestem were common. Blue grama made up 91% of the basal cover on the xeric uplands of the loessial hills of western Nebraska (Hopkins 1951). Buffalo grass (*Buchloe dactyloides*) and June grass were common. On the more mesic hillsides dominance was shared by side-oats grama and big bluestem (*Andropogon gerardi*). The dominants on grasslands in Kansas have been discussed for two prairies studied in this paper and on the deep soil upland areas near Hays. However, Albertson (1937) also found that the shallow soil with rock fragments supported more mesic dominants such as little bluestem, big bluestem and side-oats grama. Species of *Agropyron* and *Stipa* furnish most of the upper layer in the northern part of the mixed prairie but are replaced by the andropogons in the south (Bruner 1931). The upper layer in Oklahoma commonly consists of a mixture of side-oats grama, little bluestem and silver beardgrass while the lower layer is dominated by blue grama, hairy grama and buffalo grass. Heerwagen lists blue grama as the most important grass in the mixed prairie of New Mexico (Weaver & Albertson 1956). Other important species were buffalo grass, western

wheatgrass and galleta grass (*Hilaria jamesii*). Allred listed the same grasses as dominants in this association in Texas and added silver beardgrass and plains bristlegrass (*Setaria macrostachya*). Cottle (1931) also listed black grama (*Bouteloua eriopoda*) and hairy grama as dominants in this part of Texas. Most important highland grasses in eastern Arizona, as given by Nichol (1937), were *Bouteloua gracilis* and *Hilaria jamesii*.

Each of the faciatis described above is probably one of the most common in the area indicated. However, considerable variations probably exist in the proportionate amounts of the dominant species within each faciation. The study discussed in this paper illustrates that such variations can occur within a faciation. When these variations are well known it will be possible to do a better job of managing and conserving the grasslands of the mixed prairie.

Studies of undisturbed prairies along with those which have been subjected to different intensities of grazing are of great practical importance to people interested in proper utilization of native grasslands. Range conservationists determine the degree of degeneration of pastures due to grazing from changes in composition that occur as the result of use. Knowledge of the vegetation on relict areas can be used as a criterion for judging condition of used ranges. The variations that do occur as a result of differences in soil, topography and other environmental factors need to be determined in order to judge grazed pastures with similar characteristics.

Some writers have referred to the native vegetation of western Kansas as the short grass plains. Many areas of western Kansas are dominated by the two short grasses, buffalo grass and blue grama. However there are areas, like the ones studied, which because of soil and topographic variations support nearly as many mid as short grasses. Because of grazing, most of these mid grasses have disappeared and their area has been taken over by the short grasses, especially buffalo grass. Thousands of acres which were formerly covered by a mixture of grasses are now almost pure buffalo grass pastures.

Buffalo grass pastures are fine for protection of the soil and furnish nutritious forage for livestock but when they reach this stage of degeneration production is low. Not only does buffalo grass produce less forage than some of the other climax grasses but when grazing has been this intense the buffalo grass plants that remain have lost most of their vigor. Tomanek (1948) determined the yields on short grass pastures in western Kansas and found that a moderately grazed pasture produced over three times as much forage as a heavily grazed one. The composition of the clipping areas was not greatly different but difference in vigor of the plants was apparent.

Moderately grazed areas at both Ashland and Atwood produced nearly twice as much forage as the heavily utilized areas. In terms of practical grassland management you could allow the livestock to remove just half the forage produced on the mod-

erately grazed and leave half of it to protect the soil, conserve soil moisture and store food in the roots for future use and still get as much as if the livestock ate all the grass on the heavily grazed range.

The major portion of forage on the areas studied was always produced before the first of June. Yield before July 1 varied from 70 to 97% of total production at Atwood during the 2 years of study to 56 to 85% at Ashland. Darland & Weaver (1945) working in true prairie found that warm-season grasses gave an excellent yield in May and June but decreased to less than half this rate for the rest of the season. Working in western Kansas Riegel, *et al.* (1950) found that 66% of the seasonal yield was produced by June 12 on the short-grass type. Hopkins, *et al.* (1952) in a study on this same short-grass type found that during some seasons winter annuals are partially responsible for heavy spring yields. Albertson *et al.* (1953) found that 5 years of close clipping resulted in less yield after July 1 than moderate clipping on short grass pastures.

SUMMARY

The purpose of the study was to determine cover, composition, forage yield and root development of native vegetation on the loessial soils of northwest Kansas and the Permian red soils of southwest Kansas. The effects of grazing on these factors were also studied.

Four sites, hilltop, hillside, sharp break and lowland, were studied on a native prairie near Atwood, Kansas. On the ungrazed hilltop or upland site the basal cover was only 28.6% and was dominated by the 2 short grasses, buffalo grass and blue grama, which comprised 59.4% of the cover. Some mid and tall grasses were found growing in favored locations and made up 32.4% and 8.2% of the cover, respectively. The hillside of the same prairie had a plant cover of 27.7% composed of 27.8% short grass, 69.4% mid grass and 2.8% tall grass. The sharp, rocky breaks at the base of the hillsides were dominated by 2 mid grasses, side-oats grama and little bluestem, which together furnished 93.4% of the sparse cover. The lowlands had a cover of only 17.1% composed of 35.4% tall grass, 62.8% mid grass and only 1.8% short grass. The principal tall grass of the lowland was big bluestem.

The species at Asland were similar but the relative amounts of short, mid and tall grasses were different. The upland with a cover of 32.1% had only 26.6% short grass but 73.4% mid grass. Besides blue grama and buffalo grass, hairy grama became an important part of short grass population at this location. The hillsides with an average cover of 22.2% had only 17.2% short grass, 81.9% mid grass and 0.9% tall grass. The sharp breaks had 24.3% short grass, 68.0% mid grass and 7.7% tall grass. The sparse cover of 16.2% on the lowlands was composed of 52.1% tall grass, mostly big bluestem, 39.6% mid grass and only 8.3% short grass.

Forage production in 1952 on the nongrazed prairie

at Atwood varied from 3,274 lbs/A on the lowland to 2,463 lbs on the upland and 1,902 lbs on the hillside. The continuing drought reduced production in 1953 tremendously sometimes as much as 1,000 lbs/A. From 70 to 78% of the forage was produced before July 1 in 1952 and from 80 to 97% during the same period in 1953. Yields at Ashland followed about the same trends except that they were slightly lower than those at Atwood.

Roots of prairie plants extended deeply into the permeable, loessial soil at Atwood. Most forb roots reached depths of 9 to 18 ft and grass roots 6 to 10 ft. Roots at Ashland were limited in their depth of penetration by a rock layer about 6 ft below the soil surface.

Grazing exerted tremendous changes on the vegetation. Generally, basal cover increased as grazing intensity increased. Most mid and tall grasses decreased and short grasses, especially buffalo grass, increased with grazing. This species increased from 5% under non grazing to 90% with heavy use at Ashland and from 16 to 90% under the same conditions at Atwood. Heavily grazed pastures were consequently nearly pure short grass but pastures used moderately retained many of the mid grasses.

Heavily utilized pastures often produced less than half as much forage as non-grazed prairies. Reduction of yield under moderate use was very small and some sites on moderately grazed pastures outyielded those under non grazing.

Heavy use reduced the number and depth of penetration of roots of grasses and forbs.

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COMMUNITY METABOLISM IN A TEMPERATE COLD SPRING

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INTRODUCTION

The study of community metabolism is one means of making a functional analysis of an ecosystem. Essentially it consists of the study of energy transformation by the organisms of an ecosystem. It provides a measure of the total activity of a community just as a study of individual metabolism does for an individual organism.

The present study of the relatively simple ecosystem of a cold spring was undertaken to provide a more exact measurement of community metabolism than had been available. It should be emphasized, however, that in the present state of our knowledge of community metabolism considerably more assumptions have to be made in order to present a complete picture than would be the case in many other fields.

Studies of community metabolism have been generally made either in terms of energy or of biomass (either as biomass itself or in terms of a portion of the biomass such as protein or fat). The author follows the lead of Macfadyen (1948) in believing energy units to be preferred in studies of community metabolism.

Biomass units are less suitable because there is recirculation of matter in the ecosystem and because the rates of turnover are so different for different sizes and species of organisms. Macfadyen (1948) has shown that confusion often results from the fact that many authors fail to see the distinction between the cycle of matter in a community and the flow of energy through a community. For example, Gerking (1954) states that the variability in quantity of fat in organisms makes calories an unsuitable unit for production studies.

Energy enters the organic world in the form of

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sunlight which is absorbed by the green plants and this energy is then used by those plants and by the organisms which feed upon the plants to do their internal and external work. The energy which enters the ecosystem in the form of heat is not usually important. Warm-blooded animals, if their body temperature is maintained by their environment expend less energy in keeping themselves warm. However, this effect is not important for several reasons: (1) the temperature range of all animals is small; (2) most animals are not warm-blooded; (3) related animals which live at and are adapted to different temperatures tend to have a similar rate of metabolism (Bullock 1955); (4) experiments with large domestic animals have shown that the amount of energy saved by environmental heating of the animal's body is negligible.

There are two essential points about the transfer and use of energy that need emphasis. The first is that according to the law of conservation of energy, whatever energy is used by the organisms in doing work will appear as a definite amount of heat which is lost as far as the organisms are concerned. The second is that whatever path the chemical reactions follow, an identical amount of energy is released in the oxidation of a unit amount of an organic compound.

In practice it is not possible actually to measure the increase in heat that results from the organisms' transformation of energy. It is necessary to calculate the calories transformed from data obtained through respiratory rate measurements. This can be done with the aid of the average oxy-caloric coefficient determined by Ivlev (1934) since all of the energy that an aerobic organism uses is derived from the oxidation of organic compounds. Allowance must be

made for the respiration of that biomass which was produced within one sampling interval and which also died within that interval and so did not appear in any sample (Birch & Clark 1953).

The trophic level concept of Lindeman (1942) has been used in this paper although it has been modified to meet the objections of Ivlev (1945) by considering each important species separately and by dividing the energy flow, for a population that functions to an important extent on more than one trophic level, among the levels concerned. Lindeman's methods of quantifying his trophic level analysis, used also by Dineen (1953), are open to many criticisms (Birch & Clark 1953, Macfadyen 1948) and in this study more accurate methods have been used.

The calculation of various ratios is of value in comparing the energy flow in different species and different communities. The terms in these ratios are defined here as follows: "Assimilation" is the rate of energy assimilation by a population; "Energy Transformed" or "Respiration" is the rate of energy use; "Net Production" is the difference between the previous two. "Gross Production" is used only in reference to primary producers and refers to the energy fixation (Odum 1956).

The ratio, $\frac{\text{net production}}{\text{assimilation}}$, is commonly used by

those interested in the amount of potential food that a population can produce. This is the efficiency with which energy is fixed in the organic matter of a population or trophic level and made potentially available as food to other populations or trophic levels.

The ratio of respiration to assimilation is also used. To the energy assimilated in a time unit must be added the energy equivalent of any decrease in standing crop within the period since such a decrease represents a mobilization of energy previously assimilated and stored in the bodies of organisms.

The ratio of respiration to assimilation is also used. R. S. Miller for their interest and helpful suggestions, also to Selwyn Roback, H. K. Townes, C. J. Goodnight and Arthur Clarke for help in identifying the fauna. The cooperation of the Root family who own the spring is gratefully acknowledged.

THE COLD SPRING

Small, constant temperature springs are as nearly perfect systems for the study of community metabolism as can be found in nature. They have the advantage of a comparatively unchanging chemical and physical environment, which reduces the difficulties of measurement and makes laboratory experiments simpler, for it is easier to duplicate constant conditions than varying ones. Also, the biota in cold springs has fewer species than do most communities.

In spite of these advantages, the ecology of springs, especially cold springs, has not received much attention in the United States. The faunas of the hot springs of this country were studied by Brues (1928). Dudley (1953) has investigated the faunas of some springs of varying temperature and Odum has worked

with the rich cold springs of Florida (Odum 1957).

The spring chosen for this study of community metabolism is a limnoecene, a spring in which the water emerges into a basin, located on Intervale Farm belonging to the Root family in Concord, Massachusetts. It lies at the foot of a bank of glacial till which extends laterally for about one mile and from which emerge a number of rheocrenes, springs which form brooks immediately. The basin of Root Spring is about 2 m in diameter and the water, which comes out of the ground around the uphill edge and flows out in a springbrook on the opposite side, is 10-20 cm deep. Most of the bottom is covered with mud and it is in the mud that the organisms are found. As is the case with most springs there is no true plankton.

The spring was sampled from June 1953 until November 1954, although general observations extended from February 1953 to March 1955.

November 1953 through October 1954 was the period chosen for the analysis because the emergence of the insects was over for the year by November and hence egg laying by the insects was also completed.

Environmental Conditions.—Figure 1 gives a summary of the conditions within the spring from August 1953 to July 1954. Since there was no very unusual weather during this year, it seems likely that the observed conditions were typical. The fauna and flora were subject to little in the way of changes in their physical and chemical environment. The temperature varied at most 2° C from the mean annual air temperature for the Concord region, 9.5° C. The high concentration of CO₂, 20-30 ppm, had no adverse effect on the spring fauna as far as could be observed although it may have had an important effect in excluding intolerant species. The same may be said for the oxygen concentration which ranged from 26-65% of saturation.

The Flora.—The flora of Root Spring from June 1953 to November 1954 consisted entirely of benthic algae and the duckweed, Lemna. During November and December there were only a very few diatoms present. In January the flora began to increase and the first species to appear in abundance was one of the diatoms, Eunotia, which grew on all of the available solid surfaces. As the amount of light per day increased, filamentous green algae appeared in masses all over the bottom of the spring. *Stigeoclonium stagnatile* was the principal species, along with a smaller amount of *Spirogyra* sp. By May these species had decreased in numbers and a colonial green alga, *Tetraspora lubrica*, and a tiny diatom, *Nitzschia denticula* (?), made up the main biomass of the flora. As summer progressed the green algae all diminished in abundance and the benthic diatoms were the only plants of importance. In the autumn *Spirogyra*, and *Oedogonium* and *Coleochaete soluta* formed a considerable part of the green plant flora along with the diatoms.

Lemna covered the edges of the water out of the current in the early part of the year and was mostly

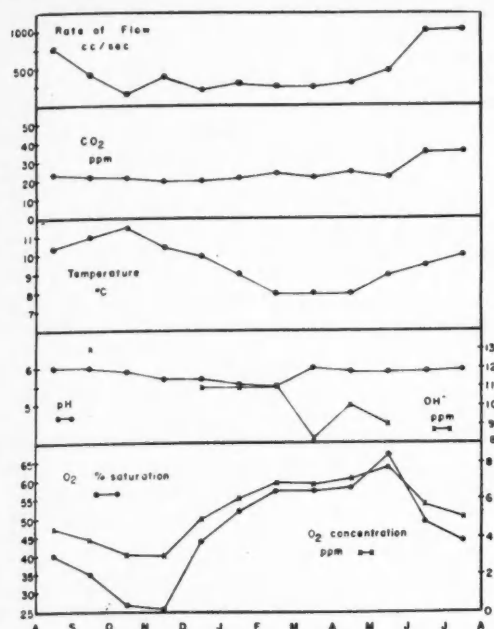


FIG. 1. Physical and chemical characteristics of the water in Root Spring, Concord, Mass., 1953-54. All data are plotted as monthly averages.

gone by April. It did not seem to contribute much to the spring community because, instead of sinking to the bottom of the springpool, it was washed out of the outlet and down the springbrook when the rains of March and April agitated the water.

While the algae contributed a considerable amount of energy to the animal populations, the main source of food, as will be shown below, came in the form of plant debris, mostly leaves from apple trees, which collected on the bottom of the spring.

The Fauna.—Although over 40 species of animals were identified from Root Spring, there were relatively few species that occurred in numbers and sizes large enough to be important in the energy balance. The most abundant animals were those which fed on debris and algae, taking mud into their gut and assimilating the digestible material. These included the oligochaete, *Limnodrilus hoffmeisteri*; and the chironomid larva, *Calopsectra dives*. Also feeding upon detritus and debris were the isopod, *Asellus militaris*, the amphipod, *Crangonyx gracilis*, and the fingernail clam, *Physa virginiticum*. The snail, *Physa*, feeds on detritus and on algae which it scrapes off of the surface of the mud. The caddis larvae, *Frenesia difficilis*, *F. missa*, and *Limnophilis* sp. eat larger bits of vegetation.

Another chironomid, *Anatopynia dyari*, eats other animals but when this food is in short supply it can get along on plant material. Other predators were the planarians, *Phagocata gracilis* and *P. morgani*.

Root Spring differed from the characteristic cold

spring described by Pennak (1954) in lacking leeches and black fly larvae and having planarians in abundance.

A list of all of the organisms found in the spring which were identified follows:

Algae

Chlorophyta

- Stigeoclonium stagnatile* (Hazen)
- Coleochaete soluta* (Brebisson)
- Tetraspora lubrica* (Roth)
- Spirogyra* sp.
- Oedogonium* sp.
- Closterium* sp.

Chrysophyta

- Cymbella aspera* (Ehrenberg)
- Nitzschia denticula* Grunow
- Stauroneis phoenicentron* (Nitzsch)
- Eunotia* sp.

Cyanophyta

Higher plants

- Lemna minor* L. (?)

Protozoa

- Euplotes* sp.
- Paramecium* sp.
- Rhabdostyla* sp.
- Vorticella* sp.

Platyhelminthes

- Phagocata gracilis woodworthi* Hyman
- Phagocata morgani* (Stevens and Boring)

Gastrotricha

- Chaetonotus* sp.

Rotatoria

- Trichocerca* sp.
- Lepadella* sp.

Nematoda

- Monhystera* sp.
- Plectus* sp. (?)

Nematomorpha

- Gordius* sp.

Annelida

Naididae

- Chaetogaster langi* Bretscher

Tubificidae

- Limnodrilus hoffmeisteri* Claparède
- Pelosciolex* sp.

Mollusca

- Physa virginiticum* (Gmelin)
- Physa* sp.

Crustacea

Copepoda

- Cyclops vernalis* Fischer
- Canthocamptus staphylinoides* Pearse
- Eucyclops agilis* (Koeck)
- Paracyclops fimbriatus* (Fischer)

Ostracoda

- Eucypris* sp.

Isopoda

- Asellus militaris* Hay

Amphipoda

- Crangonyx gracilis* Smith

Arachnoidea

Hydracarina
(Parasite of *C. dives*)

Insecta

Collembola

Tomocerus sp.

Ephemeroptera

Megaloptera

Sialis sp.

Trichoptera

Frenesia difficilis (Milne)*Frenesia missa* (Walker)*Limnophilis* sp.*Lepidostoma* sp.

Coleoptera

Agabus sp.*Bidessus* sp.

Diptera

Calopsectra dives (Johannsen)*Calopsectra zantha* Roback*Anatopynia dyari* (Coquillett)*Anatopynia brunnea* Roback*Pentaneura carnea* (Fabr.)*Prodiamesia olivacea* (Meigen)*Tendipes tuxis* Curran*Brillia parva* Johannsen*Metriocnemus hamatus* (Johannsen)*Hydrobaenus obumbratus* (Johannsen)*Tanytarsus fuscicornis* (Malloch)*Erioptera septemtrionis* O.S.*Psychoda* sp.*Eucorethra* sp. (?)*Pericoma* sp.*Culex apicalis* Adams*Mansonia perturbans* (Walker)

Hymenoptera

(A parasite of *C. dives*)

METHODS

Population Estimates.—A Dendy sampler (Welch 1948) was used to obtain samples of the bottom animals. A map of the spring was covered with a numbered grid and successive sampling sites were chosen from a table of random numbers. The samples were placed in a 16 mesh per centimeter sieve and the mud and fine debris removed by washing in the spring.

The animals were separated by hand under a magnifying lens from the mass of tubes and debris that remained. The individuals of each species were counted and the live weight determined after removal of excess water with filter paper.

The Phagocata presented a special problem because they secreted mucus when handled and because their epidermis permitted rapid water loss. They were placed on a fine screen and excess water was removed with filter paper. The screen with the animals was then weighed, the animals quickly removed with forceps, and the screen reweighed.

After counting and weighing the animals, with the exception of less than 1% used in experiments,

were returned to the spring in order to minimize disturbance of the community.

Weight was converted to calories by oxidation with potassium dichromate in sulfuric acid (Ivlev 1934). The nitrogen content of the animals, needed for this method, was taken from the literature or found by Nesslerization.

The numbers of adult insects that emerged from the water from April to October were measured with tent traps of $\frac{1}{3}$ m² or $\frac{1}{10}$ m² area.

Some attempt was made to determine the relative number of bacteria in the spring. This was done following the method of Henrieci (1936) by putting clean slides about one-fourth of their length into the mud and determining the time required for a coating of bacteria to grow.

Respiratory Measurements.—Rates of respiration of the principal animals were measured by the method of Ewer (1941), with the spring serving as a constant temperature bath. Animals were taken from the spring with as little disturbance as possible and quickly transferred to 20 cc syringes filled with spring water. The oxygen content of the water was then measured with the Micro-Winkler technique (Fox & Wingfield 1939). The syringes were placed in the spring and after sufficient time had elapsed for a measurable change to occur but not so long that oxygen tension was appreciably lowered (1-3 hrs) the oxygen content of the water was again determined. During the interval the water was usually kept sufficiently stirred by the activities of the animals themselves but if this was not the case, the syringes were turned over at regular intervals. This procedure measured the respiration under the same conditions of temperature, oxygen, pH, alkalinity, etc. as those which the animals normally experienced. At the end of the measurement the animals were taken to the laboratory and weighed. Oxygen consumption was converted to calories with the average oxy-caloric coefficient of Ivlev (1934), 3.38 calories per milligram of oxygen. This average coefficient was used as the respiratory quotient was not known.

Since two of the species studied, *Calopsectra* and *Limnodrilus*, normally live in tubes, measurement of their oxygen consumption with the animals out of their tubes and in the syringes could be subject to error. Walshe-Maetz (1953) found, however, that while the oxygen consumption of *Chironomus plumosus* was different at oxygen concentrations below 25% saturation if the animals were removed from their tubes, at higher concentrations there was no significant difference. Since the oxygen concentration in the spring never fell below 25% saturation, the above possibility of error may be safely neglected.

Molting Losses.—When an arthropod molts it leaves a certain amount of energy behind in the material of the cast off exoskeleton. Midge larvae were kept in the laboratory and weighed daily. The loss of weight after a larva-to-larva molt represents the amount of material lost with the cast skeleton. The larva-to-pupa-to-adult transition was treated as one

process. The loss of weight between the prepupal larva and the adult represents the material lost in the larva-to-pupa molt, the material lost in the pupa-to-adult molt and loss due to pupal respiration.

Oxygen Changes Due to Respiration and Photosynthesis.—Changes in oxygen due to the combined activities of all organisms living in the spring were measured by determining the changes in oxygen in the water enclosed by glass cylinders 17 cm in diameter which were pushed into the mud until they projected only 2-4 cm above the water surface. They were then filled to the top with water and covered with a glass plate. The top edge of the cylinder was ground so that the fit would be air tight. The water was sampled from all levels within the cylinder and the oxygen content measured by the standard Winkler technique at the beginning and again after a period of about 24 hours. Oxygen gradients that may have formed within the cylinder caused no appreciable sampling error. Their possible effect on the organisms was ignored.

Respiration was then measured during a period of several hours with a black box covering the cylinder to prevent any photosynthesis. By subtracting the respiration due to the macrofauna, the respiration of the decomposers, microfauna, and algae was determined.

Portion of Food Assimilated.—To find out how much potential food was not assimilated in the feeding process, *Anatopynia* larvae, kept at 9° C in spring water, were weighed and given weighed amounts of live *Calopsectra* or *Limnodrilus* every second or third day. The respiration of *Anatopynia* during the experiment was measured.

The portion of food assimilated was calculated from these measurements on the assumption that the difference between the energy contained in the food and the energy contained in the tissue added by growth plus the animal's respiration represented loss on the form of feces and in the form of material from the prey which was killed but which never entered the predator's gut.

The feeding efficiency of *Phagocata* was determined in a similar manner. There was a difference, however, in that most of the loss which occurred during the feeding activities of *Phagocata* was due to the large quantities of mucus that were secreted by the animals in their movements in search of food and in their actions in subduing their prey.

Anatopynia larvae are stated to be carnivorous (Johannsen 1937, Pennak 1954) but the present observations showed that they also digested plant food. Larvae were anesthetized each month, the contents of their guts examined under a compound microscope and the portion of animal and plant food estimated. As much could be seen in the gut of the live animal as could be observed by examining the guts of intact, cleared animals or examining food removed from larval guts. Only a relative measure of the amounts of the various types of food that were taken could be obtained with any of these methods. Difficulties

were encountered in identifying the contents of the gut and in estimating the amount of food that was represented by the portions that remained.

Measurement of Mortality.—In order to determine completely the energy flow through a population it is necessary to know what quantity of energy is lost by the death of organisms from whatever cause between periods of sampling.

Each month's sample mean was assumed to represent the actual population on the midday in the month. A sampling interval extended, therefore, from the 16th of one month to the 15th of the next.

An estimate of the mortality between samples was obtained with the use of the equation given by Ricker (1946): $P_t = P_0 e^{(k-i)t}$ in which k is rate of growth or net production; i is rate of mortality; P_0 is weight of population at time zero; P_t is weight of population at time t ; t is taken to equal one month.

Values for k were determined by raising animals in a 9° C cold room and by estimation from the greatest rate of increase that occurred in the natural population. In those populations which did not reproduce during the summer, k was determined from the average increase in weight of surviving individuals.

Once k was determined it was used as a constant (except in the cases of *Calopsectra* and the *Trichoptera* where it was determined each month by the last method mentioned above). Net production was probably about the same at all seasons of the year for most animals in the constant conditions of the spring. It makes no difference in calculating energy flow whether the net production of a population takes the form of growth of individual organisms or of increase in numbers of individuals (i.e., reproduction).

A value for i was found for each sampling interval from the above equation and multiplied by the average population (geometric mean) during the interval to give an estimate of mortality. This mean is not so exact as that given by Ricker (if i is constant for the interval considered) but it is easier to calculate. Actually, i is a continuous varying quantity rather than constant for any month and use of the geometric mean is accurate enough for this study.

Since the data for energy flow were compiled on basis of the calendar months, the total mortality was divided between the two months involved according to the ratio of the geometric means of the populations present in the second half of the first month and the first half of the second month (assuming each month to contain 30 days). The mortality is a minimum estimate since the mean of the populations present during each was used in the calculations as if it were the true value on the fifteenth of the month. This use tends to smooth out the curve of population size.

Input of Energy in the Form of Organic Debris.—The amount of debris that fell into the spring was estimated by placing a box having sides 30 cm high and a bottom area of $\frac{1}{10}$ m² on the ground next to the spring and collecting the material that accumu-

lated in the box. This material, mostly leaves, twigs, fruit, etc., was dried and weighed and its caloric content determined.

The organic matter in the inflow and outflow of the spring was measured following the method of Pennak (1946).

SPECIES POPULATIONS

The results will be presented and discussed separately for each species that was individually studied. These data will then be combined to give a picture of the community metabolism for the spring as a unit. The actual sampling data may be found in a PhD thesis deposited in the Biology Library, Harvard University.

Calopsectra (= *Tanytarsus*) *dives* (Johannsen).—This species is one of the two abundant chironomids in the spring and is a typical member of this genus characteristic of oligotrophic waters. The population of *Calopsectra* during the study is shown in Fig. 2 and Table 1. There were no larvae of this species during the winter. A maximum standing crop of 87.6 KC/m² was reached in August after which pupation and emergence of adults reduced the population again to zero. The population means for June, July and August differ significantly at $P = 0.01$. The calories contained in the standing crop were found to be $0.69 \text{ KC/gm} \pm 0.020$ (12 determinations).

Fig. 2 also shows the number of adults that emerged and the monthly totals are given in Table 1. The sex ratio among the adults was 53% female and 47% male (based on 1500 adults).

Because mating and egg laying take place so soon after emergence it was estimated by observing the insects that about two-thirds of the females laid their eggs in the spring from which they had just emerged and the others dispersed. By counting the eggs contained in 5 virgin females it was found that they laid an average of 250 eggs each.

The number of eggs that gave rise to the 1954 population was calculated from emergence data for

TABLE 1. Population of larvae and emerging adults of *Calopsectra dives* in Root Spring, Concord, Mass., in 1954. Energy content is estimated on the basis of 1.58 cal/mg as determined for *Anatopynia dyari*.

	Jan.- April	May	June	July	Aug.	Sept.	Oct.- Nov.
Larvae							
Number in thousands/m ²	1.7	89.5	65.0	57.0	0.2
Weight in gms/m ²	3.0	58.5	82.4	127.0	0.2
Energy content in KC/m ²	2.1	40.4	56.8	87.6	0.1
Adults							
Number/m ²	13	170	953	3464	13250	533
Weight in mg/m ²	12	156	876	3170	12200	490
Energy content in KC/m ²	0.019	0.246	1.38	5.00	19.30	0.775

1953. Fifty-eight hundred females emerged at that time and these females at 250 eggs apiece laid roughly 980,000 eggs per square meter.

The mortality of larvae calculated from Table 1 for July to August was 15% and for June to July, 28%. Thirty percent, therefore, will be used for mortality from May to June when the larvae were smallest. This figure agrees with the mortality rates of young chironomid larvae given by Borutzky (1939). Most of these larvae did not appear in the samples in May because they were so small that they passed through the meshes of the sieves. On the basis of 30% larval mortality 128,000 larvae emerged from eggs in May. As 980,000 eggs were laid, 87% of these did not survive to hatch.

As no new larvae hatched during the summer, all of the individuals are of about the same age and mortality is easily calculated with the formula:

Mortality = antilog

$$\left(\frac{(\log P_0 - \log P_t)}{2} \right) \left(\frac{(\log P_p - \log P_t)}{\log e} \right).$$

The first expression gives the average population present during the interval and the second gives the

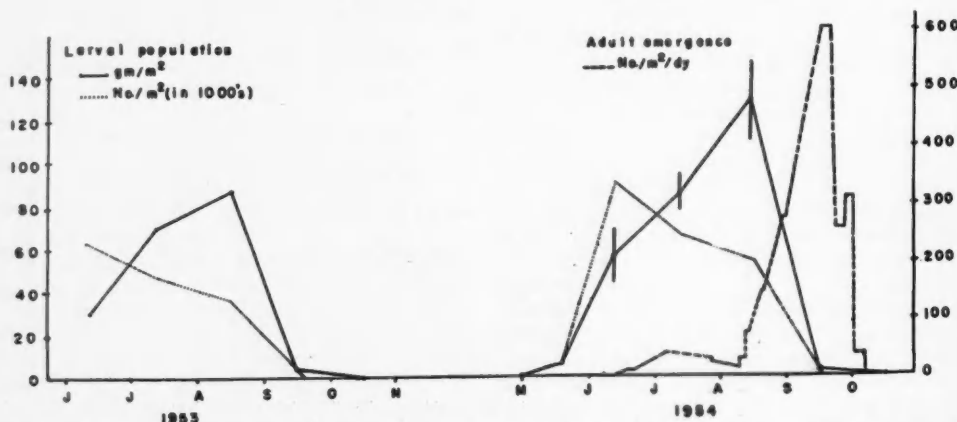


FIG. 2. Size of larval population and adult emergence for *Calopsectra dives* in Root Spring, Concord, Mass. Vertical lines represent 95% confidence limits.

death rate. P_0 is the size of the population at the beginning of the instar; P_t the size at the end of the instar; and P_p the theoretical size of the population at the end of the instar had there been no mortality. To facilitate the calculation, Table 2 has been set up.

TABLE 2. Data for calculation of mortality of *C. dives* larvae (per square meter). The value of P_0 for May is taken from the total estimated larvae hatching multiplied by the calories per egg (.002). The value for P_t in August is the total calories contained in the larvae that successfully emerged as adults.

	Instar	No. of larvae	P_0	Gram cal. larvae at end instar	P_t	P_p
May 15 to Jan 15...	1	128,000	0.256KC	.45	40.4KC	57.6KC
Jun 15 to Jul 15...	2	98,500	40.4	.86	56.8	76.5
Jul 15 to Aug 15...	3	65,000	56.8	1.54	87.6	103.1
Aug 15 to Sep 15...	4	57,000	87.6	2.09	28.8	119.1

Mortality was divided among the calendar months as described previously except for that calculated for the last instar which was divided among August, September and October in proportion to the adult emergence. Most of the deaths during this interval occurred as the pupae tried to wriggle out of the larval tubes and were caught in the mucus which the increased numbers of planarians had spread over the tube mouths.

The energy lost by respiration is, in a sense, the most important part of the energy flow through the population since this is the energy that the animals actually use in their life processes. From 9 measurements the respiratory rate of *Calopsectra* was found to be 0.475 ± 0.022 mg O_2 /gm/hr or 1.67 ± 0.08 cal/calorie of larva per month.

With the data presented above it is possible to draw up an energy balance sheet for the population of *Calopsectra dives* during the summer of 1954 (Table 3). Calculation of the respiration of animals that died between samplings was based on an average life of one-half month (i.e. mortality uniform with time). The sum of the energy assimilated by the population of *Calopsectra dives* was 520.3 kilo-calories per square meter. The larvae transformed 389.6 KC, about 75% of the input.

Some of the energy carried out of the system in the bodies of the adults was used in the life processes of the adults and some of the energy contained in the female adults was in the eggs and would have been used by the developing embryos. Therefore, about 80% of the input energy was transformed to heat by the midges.

The efficiency, $\frac{\text{net production}}{\text{assimilation}}$, of the *Calopsectra* was 100% minus 80% = 20% since this is the amount of energy that the population passes on to other populations.

Anatopynia dyari (Coquillett).—*Anatopynia* is the second most abundant species of midge occurring in the spring. Figs. 3 and 4 and Table 4 show the size of the population of *Anatopynia* larvae which varied

from a low of 4.4 KC/m² in September during pupation and adult emergence to a high of 28.2 KC/m² in October. These figures include two species other than *A. dyari*; *Anatopynia brunnea* Roback and *Pentaneura carnea* (Fabr.). Both of these latter species are similar in habits to *A. dyari* and were less than 1/5 as numerous.

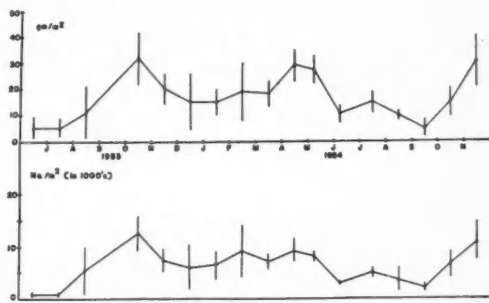


FIG. 3. Population of *Anatopynia* larvae in Root Spring, Concord, Mass. (The vertical line indicates the 90% confidence limits of the mean.)

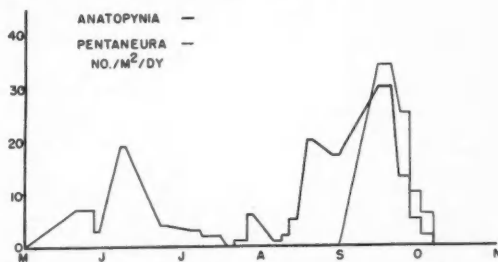


FIG. 4. Emergence of adults of *Anatopynia* (heavy line) and *Pentaneura* (light line) from Root Spring, Concord, Mass. in 1953-54.

The energy content of the larvae was found from 6 determinations to be 0.88 ± 0.056 KC/gm.

The differences in numbers of individuals between May and June, June and July, July and September 1954 and October and November 1953 were significant at $P = 0.01$ and between September and October 1954 at $P = 0.05$.

It was estimated from field observations that about 1/4 of the emerging females lay their eggs in the spring. Since there are no other springs in the vicinity from which *Anatopynia* adults could reach Root Spring, 264 females which emerged in May and June deposited 23,100 eggs and 980 females which emerged in August and September deposited 86,100 eggs. (Five virgin females were examined and found to contain 325, 340, 350, 370, and 375 eggs, or an average of 350 eggs each.)

By examination of the graph of the numbers of individuals of *A. dyari* (Fig. 3) the mortality of the eggs and the very young larvae can be estimated. From November through May 15 there were about 7500 larvae/m². From May 15 through July, 510 adults emerged but between May and June there

TABLE 3. Balance sheet for energy flow in *Calopspectra dives* in Root Spring, Concord, Mass., in kilo-calories per square meter. Column 4 shows the calories respired before molting by the biomass represented in the deposited larval skins. Values for deposits were measured for *A. dyari* and assumed proportional for *C. dives*.

Month	Standing crop	Respiration of S. C.	Respiration of animals that died	Respiration of deposit	Emergence	Pupal deposit	Larval deposit	Mort.
October to April.....
May.....	2.1	3.5	0.02	0.01
June.....	40.4	67.5	0.6	3.3	0.25	0.11	4.0	0.7
July.....	56.8	95.0	1.0	4.8	1.38	0.61	5.7	1.2
August.....	87.6	146.2	12.4	7.3	5.00	2.2	8.8	14.9
September.....	0.1	0.2	45.8	19.30	8.5	54.8
October.....	1.8	0.78	0.34	2.1
		312.6	61.6	15.4	26.7	11.8	18.5	73.7

Net change in standing crop.....0
 Total respiration.....389.6
 Total assimilation.....520.3

TABLE 4. Monthly summary of larval population and adult emergence of *Anatopynia dyari* and *Pentaneura carnea* in Root Spring, Concord, Mass., 1953-54. Larvae of the two species were not distinguished.

	1953			1954										
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.
Larvae														
Number in 1000's...	12.4	7.2	6.0	6.3	8.9	6.8	9.1	8.1	2.6	5.1	3.8	2.0	6.6	10.9
Energy content in KC/m ²	28.2	17.6	13.2	12.3	15.8	15.8	25.5	16.7	9.7	13.2	8.8	4.4	13.2	27.3
Adult														
Anatopynia														
No/m ²	128	308	73	308	633	15	...
Mg/m ²	311	599	129	642	1188	31	...
Pentaneura														
No/m ²	646	40	...
Mg/m ²	667	41	...

was a decrease in the population of 4500 larvae/m². This indicates that 3990 larvae died in this interval. This decrease is reflected in the curve for weight/m². Newly hatched larvae did not appear in the samples until about one month after the eggs were laid.

In July the numbers/m² increased to 5000, representing an addition of 2000 new larvae from the 23,100 eggs laid during May and June. A mortality of 91.4% occurred among the eggs and young larvae. In November somewhat more than 10,000 new larvae appeared indicating a mortality of 88% of the autumn eggs and young larvae. On the basis of a three to one ratio for the mortality of eggs to the mortality of young larvae (from the data of Borutzky 1939 for another species of chironomid), it was calculated that these larvae stored a total of about 0.4 KC/m² in their bodies before they died, and this amount is included in the tabulation of energy flow. This calculation is very rough since exact data are not available, but it is certain that the effect of these young larvae did not materially affect the total energy flow for this species, 239.2 KC/m².

A few determinations were made of the amount of energy lost in the molted exoskeletons of the larvae.

A. dyari was used for these measurements because of their large size and good viability under repeated handling. Three larva-to-larva molts were successfully measured. The loss was 11.5%, 10% and 9%, or an average of 10% loss of energy/molts in terms of the final larval weight. This agrees well with the figure of Borutzky (1939) for *Chironomus plumosus* who found a loss of 16.8% in all three molts in terms of the final larval weight. A loss of 10%/molts is equal to 16.3% loss in three molts.

There is a similar loss of energy in the transformation from prepupal larva to pupa and then to adult. It was found that an adult midge came from a larva which contained 1.44 times as many calories as the adult. Thus 0.44 cal/cal of adult were deposited with each adult emergence.

It was apparent, after examination of larvae from the spring and raising larvae successfully on a diet of Spirogyra, that *A. dyari* larvae are both herbivores and carnivores. The larvae may not, however, be able to exist solely upon detritus. During December and January when algae were scarce and the larvae were not obtaining much animal food, their average weight decreased. The approximate portion of the

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food of *A. dyari* larvae which came from animal sources was as follows: none in January; one-eighth in April, one-quarter in November, December, March, July and October; one half in May, June and August; three-quarters in February and September.

It will be seen when the predator-prey balance for the entire community has been presented that the estimation of the proportions of foods from the two sources must be at least approximately correct.

When detritus-feeding forms eat, they take into their guts a variety of material usually in small bits and their digestive enzymes act on the mass of material to make available for absorption all the potential food. The only organic material that passes through is that which is indigestible, considered by many workers to be the crude fiber portion of the organic matter (Lindeman 1942, Birch & Clark 1953). When the food is animal prey, however, unless the predator can swallow the prey whole, a certain amount of it will be lost without ever entering the alimentary canal. This waste was measured for *A. dyari* feeding on *Calopsectra* and *Limnodrilus*.

Thirty duplicate experiments revealed that when feeding on animals *A. dyari* are able to assimilate, on the average, only 30% of their prey ($29\% \pm 2\%$). The remaining 70% is lost in the form of (1) blood of the prey which passes into the water, (2) flesh which is not swallowed by the predator, and (3) indigestible material which passes through the predator in the form of feces. This figure seems reasonable when it is realized that *Anatopynia* grab their prey in their mandibles and draw it into their esophagus bit by bit. The skin of the prey is ruptured in the process and blood escapes. Since the mouth of *Anatopynia* is smaller than the usual prey, a large amount of the flesh is also lost. The loss may be less when *Anatopynia* feeds on animals which are small enough to be swallowed whole.

Measurements of respiration of the larvae of this species were made in Root Spring throughout the year. Eighteen measurements gave a mean of 0.45

± 0.04 mg O_2 /gm fresh wt/hr or 1.24 calories respired/calorie of larvae/month. The figures for respiration in the balance sheet (Table 5) are corrected for mortality and deposit as explained for *C. dives*. The net change in the standing crop for the year was found by subtracting from the increases the decreases due to deposit, emigration, and mortality. Mortality was calculated from the differences in the standing crop and deposit and emigration. Mortality and increases in the standing crop were divided between months in proportion to their standing crops. Energy obtained from cannibalism was figured as $\frac{1}{2}$ mortality on the basis of the feeding efficiency. Except for August when there were a large number Phagocata present, the mortality of *Anatopynia* was probably due to cannibalism since this chironomid was the most abundant predator present. In December and January the mortality may only be respiratory loss as there was no significant decrease in numbers during those months.

The total assimilation of energy by *Anatopynia* larvae for the year of the study, 249.1 KC/m², was found by adding losses due to respiration, death, deposits of larval and pupal exuvia, and emigration of adults. Of this total assimilation 9.9 KC came from cannibalism and 3.2 KC from a decrease in the standing crop, leaving 236.0 KC which came from sources outside the *Anatopynia* population.

The proportion of energy transformed by *Anatopynia* is $\frac{208.5 \text{ KC respired}}{249.1 \text{ KC assimilated}}$ or 84%. Their efficiency at passing energy containing material to other populations is $\frac{30.7 \text{ KC passed on to other populations}}{236.0 \text{ KC assimilated from outside sources}}$ or 13%.

Since *Anatopynia* larvae are both herbivores and carnivores, the energy flow through them may be divided into two parts in proportion to the energy obtained from animal and plant sources. This was done in the balances for these two trophic levels presented below.

TABLE 5. Energy balance sheet for *Anatopynia* in Root Spring, Concord, Mass. for 1953-54 (in kilo-calories per square meter).

Month	Standing crop	Larval deposit	Pupal deposit	Emigration	Mortality	Energy from Cannib.	Respiration	Increase in S. C.	Energy from animals	Energy from algae
Oct. '53	(28.2)	(1.4)
Nov.	17.6	1.0	6.1	2.0	21.4	...	4.9	14.5
Dec.	13.2	2.5	2.5	16.4	...	3.5	10.4
Jan. '54	12.3	0.4	0.4	15.3	1.6	...	16.5
Feb.	15.8	19.6	1.9	16.1	5.4
Mar.	15.8	19.6	4.3	6.0	17.9
Apr.	25.5	1.6	4.5	1.5	32.6	8.0	4.8	33.3
May	16.7	1.0	0.2	0.5	6.9	2.3	21.3	...	9.5	9.5
Jun.	9.7	...	0.4	1.0	1.3	0.4	12.0	1.7	6.6	6.7
Jul.	13.2	...	0.1	0.2	2.6	0.8	16.6	2.3	4.5	13.6
Aug.	8.8	...	0.4	1.0	3.1	(1.0)	10.8	...	5.4	5.4
Sep.	4.4	...	1.3	2.9	5.5	5.5	8.2	2.8
Oct.	13.2	1.3	...	0.1	0.2	...	17.4	13.1	7.6	22.9
Nov.	(27.3)
	-3.2	4.9	2.4	5.7	27.6	9.9	208.5	37.4	77.1	158.9

TABLE 6. Population sizes in numbers per square meter and kilogram calories per square meter for animals other than chironomids in Root Spring, Concord, Mass. in 1953-54.

	1953			1954										
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.
<i>Limnodrilus</i>														
No. of animals.....	?	7600	7700	9000	10600	4800	4200	7300	4300	3700	3900	3450	3200	1300
Energy.....	23.0	32.0	30.4	32.0	53.0	17.6	18.0	30.6	16.7	16.4	23.2	21.3	18.7	3.7
<i>Asellus</i>														
No. of animals.....	1700	270	500	1100	400	100	400	100	100	200	2400	1700	900	1200
Energy.....	16.6	4.3	8.6	26.5	8.4	1.8	4.9	1.9	2.3	2.8	11.4	10.0	8.1	19.4
<i>Phagocata</i>														
No. of animals.....	1000	200	500	3300	1800	1100	300	400	500	900	2400	4600	1500	100
Energy.....	7.1	2.3	2.7	22.4	5.1	3.9	2.4	0.8	1.3	3.1	16.2	27.9	6.8	1.2
<i>Trichoptera</i>														
No. of animals.....	980	390	270	470	710	350	80	200
Energy.....	0.78	0.78	1.14	3.41	9.73	7.45	2.39	10.8
<i>Pisidium</i>														
No. of animals.....	1000	500	470	1300	2700	1500	2700	1500	1100	1900	1400	2400	3600	800
Energy.....	4.0	1.7	2.0	6.8	6.5	4.8	9.3	5.5	6.4	6.6	4.7	5.7	6.8	3.9
<i>Physa</i>														
Energy.....	0.2	0.8	1.9	3.6	1.4	1.1	1.1	0.7	1.3	0.1
<i>Crangonyx</i>														
Energy.....	0.2	1.4	0.9	0.6	1.2	0.7	0.8	0.3	4.1	0.7

Limnodrilus hoffmeisteri Claparède.—*Limnodrilus* is a typical aquatic, tube dwelling oligochaete, which reproduces throughout the year in Root Spring. It feeds upon detritus.

Table 6 gives the monthly population of *Limnodrilus*. The caloric content was found to be 0.76 ± 0.026 cal/mg fresh wt. The great decrease in population in November 1954, just after the study period, was probably caused by the action of the several hurricanes of that fall, which disturbed the spring by uprooting nearby trees.

The amount of energy transformed by *Limnodrilus*, measured by respiration, was calculated to be 1.22 ± 0.35 cal/cal fresh wt/month (0.83 ± 0.024 mg O_2 /mg/hr) from 15 determinations.

The mortality was calculated using the formula of Ricker (1946) by making the assumption that the rate of increase was constant throughout the year. Since the temperature of the water is nearly constant the year round and since it makes no difference for this calculation whether the increase takes the form of reproduction or growth, this assumption of constant rate of increase is probably quite reliable. It may be noted that the worms had full guts at all seasons.

To find the rate of increase, k , the two methods mentioned previously were used. Weighed animals confined in strained mud in the laboratory cold room were reweighed after two weeks. When one or more animals in an experiment died, the experiment was discarded. Of the 5 successful experiments the one with the maximum rate of increase, in which k equaled 0.474 for a 30 day month, was taken as the significant one since laboratory conditions were not as conducive to growth as were conditions in the spring to which this population of worms was adapted.

A value for the rate of increase was also obtained

from the increase of the natural population in the spring from April to May, $k = 0.530$. Even though the P value lay between 0.05 and 0.10 for this population increase, the larger value for k was used as it agreed fairly well with the maximum value obtained in the laboratory experiments and as k obtained from the fluctuations of a natural population will have a minimum value. The balance sheet for the energy flow through the population of *Limnodrilus* was set up in Table 7.

These tube worms assimilated a total of 644.1 KC/m² during the year of investigation. Some energy assimilated previously also flowed through the population since the standing crop decreased by 13.3 KC/m².

The oligochaetes used, in their life processes, 173.8 KC or 74% of the energy assimilated. They passed on to other populations 173.8 KC, an efficiency of $\frac{173.8 \text{ KC}}{657.4 \text{ KC}}$ or 26%.

Asellus militaris Hay.—*A. militaris* is the most common and widespread of the American species of aquatic isopods. It feeds on anything edible that it encounters although it does not ordinarily kill prey. In the Root Spring the isopods reproduced throughout the year. The population size is given in Table 6.

The figure for the conversion of moist weight to calories was calculated from the analysis of the chemical composition of *Asellus* by Ivlev (1934).

Mortality was figured using a value for k calculated from the increase in the population from July to August. The difference between these two means is significant at $P = 0.05$. An error could arise from migration into the spring since this is one of the species that could crawl up the springbrook from the pond below. However, no *Asellus* were even

TABLE 7. Energy flow figures for the animals of Root Spring, Concord, Mass., 1953-54, with the exception of the chironomids. All data in kilocalories per square meter per year.

Species	Change in S. C.	Respi- ration	Immi- gration	Morta- lity	Mucus loss	Canni- balism	Outside assimi- lation	Total energy flow	Net Produc- tion
<i>Limnodrilus</i>	-13.3	483.6	173.8	644.1	657.4	173.8
<i>Asellus</i>	3.8	486.1	104.5	604.4	604.4	104.5
Phagocata.....	-0.9	18.7	48.2	89.1	23.9	131.2	156.0	113.4
Trichoptera.....	67.5	18.3	39.2	88.4	106.7	39.2
<i>Pisidium</i>	5.1	90.9	76.7	?	172.7	172.7	81.8
Physa and <i>Crangonyx</i>	90	30	120	120	30

found in the springbrook and migration was probably insignificant. Losses due to respiration were found to be 1.22 ± 0.05 mg O_2 /mg/hr.

There is an error in the energy balance due to the fact that no allowance was made for energy lost by molting in this crustacean. The error would not come to more than 10% of the energy passed through the population and would probably be less to judge from the molting of the chironomids for which this calculation was made.

The energy balance for this species is presented in Table 7. Some energy, 3.8 KC, was stored in an increase in the standing crop during the year of study. About 80% of the energy intake of *Asellus* was used for its life processes.

Phagocata gracilis woodworthi Hyman and *P. morgani* (Stevens and Boring).—These two planarians are the only important exclusively predatory animals in the spring and feed on live or recently dead animals. Since they are able to suck in only the softer parts of their prey, the harder parts, such as the exoskeletons of arthropods, are left behind. These species were observed to have no definite breeding season and reproduced throughout the year.

Both species of *Phagocata* are considered together in the energy flow calculations because they are ecologically similar. They feed on the same sorts of material and live in the same habitat. The fact that they are members of the same genus also indicates probable similarity in ecology. They differ in size, however; *P. morgani* is seldom found to weigh more than 1.2 mg while *P. gracilis* attains a weight of 20 mg. They also differ in that *P. gracilis* has many pharynxes while *P. morgani* has only one, and in that most of the apparent "cannibalism" among flatworms in the spring is really due to *P. morgani* feeding on *P. gracilis*. The size of the combined populations is given in Table 6.

The calories per unit weight were calculated from data gathered for *P. gracilis* and assumed to be the same for *P. morgani* (1.33 ± 0.02 cal/mg). The rate of respiration was also calculated using *P. gracilis* as the experimental animal and was 0.0735 ± 0.005 mg O_2 /gm fresh wt/hr. Starvation of planarians causes their respiratory rate to vary (Hyman 1919) but was not a factor in these determinations since the animals were taken at random from the natural population.

Flatworms differ from other sorts of animals in that they secrete a great deal of mucus in their activities. They lay down a film of mucus whenever they move over objects and use it to ensnare their prey. For this reason it was necessary to measure the amount of energy lost by the *Phagocata* in the form of mucus.

Food in the form of weighed amounts of live oligochaetes was given to the worms at intervals far enough apart so that as far as could be determined by observation all of the food was consumed. It was then assumed that the difference between (1) food supply and (2) respiration, growth, and inedible parts of the food represented mucus secreted by the animals. The assimilation of food given to the worms was figured to be 90% of the prey biomass on the basis of the analyses of Birge & Juday (1922) which showed that the *Phagocata* were fed was about 10%. The results showed that *Phagocata* secreted an amount of energy in the form of mucus that was nearly equal to their body calorie content each month (0.94 ± 0.10 cal mucus/cal/month).

It is possible with the foregoing data to construct the energy balance sheet for the *Phagocata* (Table 7). Energy available from cannibalism was taken as one-half of the decrease in population of *Phagocata*. There are no other macroscopic animals which will eat flat-worms (Hyman 1951); therefore, all of the dead *Phagocata* were either eaten by their relatives or decomposed by microorganisms. It was not possible to measure mortality except by comparing the size of the standing crop in successive months. There is not enough information to explain the fluctuations in population size of these animals and no reason to assume that the rate of increase is constant throughout the year. Therefore, it is not possible to calculate mortality with Ricker's (1946) formula.

The fraction of assimilated energy transformed by *Phagocata* is very low, $\frac{18.7 \text{ KC transformed to heat}}{156.0 \text{ KC total assimilation}}$ or 12%. This is probably an adaptation made necessary by the large amounts of energy they lose in mucus which they constantly secrete. If, in calculating the fraction, the energy in the mucus is included with the energy transformed as energy "used" by

the animals, the result is $\frac{107.8 \text{ KC}}{156.0 \text{ KC}}$ or 69%, which is much closer to the fraction of energy transformation by other animals.

Including the energy secreted in mucus with the energy transformed gives a valid basis for comparison with other animals of the community as the mucus secreted is a necessary part of a planarian's existence and demands a large proportion of the energy assimilated.

The efficiency of net production compared to assimilation is $\frac{113.4 \text{ KC net production}}{131.2 \text{ KC assimilated from sources outside the population}}$ or 87%.

Caddis Fly Larvae.—The caddis fly larvae in Root Spring, *Frenesia missa* (Milne), *F. difficilis* (Walker), *Limnophilis* sp., and *Lepidostoma* sp., are considered as a unit in the energy flow picture.

Frenesia difficilis and *Limnophilis* sp. were the species most commonly found. *Frenesia difficilis* was raised from the larva and identified. *Limnophilis* was not raised to adulthood and could not be determined to species. *Frenesia missa* was collected as the adult flying around the spring and was not associated with a larva in the spring. It may have not been present in Root Spring. The *Lepidostoma* larva was rare and also not associated with an adult.

The preferred habitat of the caddis larvae was not the spring but the springbrook and there were always more larvae in the latter place. The animals in the spring were individuals that had wandered into the pool due to their orientation to the current. Very few of the pool larvae emerged as adult insects and none was collected in the tent trap set over the spring.

Caddis larvae in general are herbivorous although they will eat each other if crowded conditions prevail. The larvae of *Frenesia* feed almost entirely on roots and leaves of higher plants (Lloyd 1921) and in the spring they fed on those objects which fell into the water from the surrounding vegetation. Cannibalism among caddis larvae was not important in the present study as they were never present in numbers large enough to constitute crowding.

The population figures for the Trichoptera (Table 6) were checked by direct counting of the caddis larvae on the spring bottom. The errors are less than 10%.

All reproduction of the population occurs in the late fall and young larvae first appear in mid-winter. The increases in the number of individuals during the summer were due to immigration of larvae from the springbrook.

The caloric value of the Trichoptera was determined from one measurement which gave a value of 0.98 cal/mg fresh weight. This agrees with the data of Birge & Juday (1922) on the chemical composition of Trichoptera larvae.

The value for respiratory losses for the Trichoptera larvae was taken from the work of Fox & Baldes (1935), who found that at 10° C, larvae of *Lim-*

nophilus vittatus consumed 0.73 mg O₂/gm fresh wt/hr. The animals used by Fox & Baldes averaged 4.6 mg. Because the average weight of the Trichoptera larvae in Root Spring was 14 mg, the average rate of respiration would be approximately 0.50 mg O₂/gm fresh wt/hr (based on the theory that rate of respiration is proportional to body surface, Zeuthen 1953).

For the calculation of energy flow it was assumed that from the middle of January to the middle of March there was no immigration. The larvae at that time were very small and did not move about much. (Error from this assumption could not exceed 1% of the total energy flow for these species.) Again from the middle of May to the middle of July there was no immigration because the outlet of the spring was blocked as far as the caddis larvae were concerned. The mortality rates were calculated for those intervals when there was no immigration and assumed to be the same for the months when larvae did enter the spring and direct calculation was not possible. The constant environmental conditions give a basis for this assumption with which the energy flow balance was constructed (Table 7).

The fraction of energy transformed by the caddis larvae was rather less than for the other populations in the spring, $\frac{67.5 \text{ KC}}{106.7 \text{ KC}}$ or 64%. The value is lower

for the trichoptera in the springpool than it would be for those in the brook, since energy transformation which was not measured occurred in immigrant larvae before they entered the pool. The efficiency in terms of the energy passed on to other populations, net production over total energy flow, was 36%.

Pisidium virginicum Bourguignat and *Musculium partumeium* Say.—These fingernail clams live completely buried in the mud and feed on organic matter which they filter out of the water. While it was difficult to separate these two genera, it was believed that most of the population (Table 6) belonged to *Pisidium*.

The value for calories per unit weight of live tissue was obtained from the determinations of the chemical composition of *Sphaerium* (a fingernail clam) performed by Ivlev (1943). The respiration of these two species of molluscs was measured in three experiments with 23 animals and found to be 0.36 mg O₂/gm/hr.

The total mortality was calculated using the increase in the natural population from December to January to find a value for *i* in the formula for mortality. The difference in the mean populations for these two months was significant at *P* = 0.05.

The energy flow chart for the *Pisidium* and *Musculium* is given in Table 7. Respiration over total energy intake was 53%. The efficiency in passing organic matter on to other populations was 100% minus 53% or 47%.

Crangonyx gracilis Smith and *Physa* sp.—The amphipods and gastropods were relatively unimportant

in the economy of the spring. *C. gracilis* feeds on all sorts of organic matter, both animal and plant but rarely kills its own prey. Physa is omnivorous. Unlike many of the animals in the spring, it breeds only during those months of the year when the length of daylight is more than 13½ hours (Jenner 1951). Table 6 gives the population of these two species.

The rates of respiration and of calories per unit weight for Physa were taken from the data for Pisidium. The data for Crangonyx were taken from one measurement of each variable: calories per unit weight equaled 0.81 cal/mg fresh wt; respiratory rate equaled 1.15 mg O₂/gm fresh wt/hr or 3.4 cal/cal fresh wt/month. The latter figure is reasonably close to the rate found for the other crustacean in the spring, Asellus, which respired 3.3 cal/cal/month.

Physa and Crangonyx respired at least 47.3 KC/m²/yr and had a mortality of 9.9 KC/m²/yr (the total amount built into their tissues during the year since at the end of the period both populations were practically absent). Assuming the efficiencies of these species to be similar to those of the other molluscs and crustaceans in the spring Physa and Crangonyx together respired roughly 90 KC/m²/yr and passed 30 KC/m²/yr to other populations in the system (Table 7).

ENERGY EXCHANGE BETWEEN THE SPRING COMMUNITY AND SURROUNDING AREAS

There were several forms of energy exchange between the spring and its surroundings: (1) dissolved and particulate organic matter contained in the water which entered and left the springpool, (2) the organic matter that entered the spring in the form of leaves, other pieces of vegetation, and animals that fell into the water, (3) the adult insects that left the system when they emerged (there was no other emigration), (4) the immigration of caddis larvae, and (5) the sunlight which was used by algae for photosynthesis. (Since the heat from sunlight was of no use to the spring organisms, it was not considered.) Of these, the energy of the emergence and immigration of insects has already been calculated.

The results of determinations of the organic content of the water entering and leaving the spring showed no significant difference in kind or amount between the organic matter being carried into the system and that being carried out. Rain did not affect these determinations as surface water did not drain into the spring and there were no noticeable short-term changes in ground water flow following rains or drought.

The most important source of energy for the spring community consisted of the leaves and other plant material that fell into the water from the surrounding land. This occurred mostly in the autumn and came to approximately 2350 kilocalories/m² during the year under consideration.

MICRO-ORGANISM METABOLISM

The rates of respiration given for the microflora and microfauna were obtained from the total respiration of the benthos minus the calculated rates of respiration of the known average biomass of macrofauna (Table 8). There were two periods of maximum activity of micro-organisms in Root Spring, one early in spring and the other in autumn.

TABLE 8. Photosynthesis and respiration of micro-organisms in Root Spring, Concord, Mass.

Month	Mean rate of photosynthesis	Mean rate of respiration
	KC/m ² /month	KC/m ² /month
November 1953.....	...	17
December.....	...	17
January 1954.....	8	33
February.....	56	50
March.....	138	25
April.....	250	14
May.....	102	25
June.....	68	25
July.....	45	20
August.....	23	42
September.....	11	50
October.....	19	32
	710 KC/m ² /yr.	350 KC/m ² /yr.

The total respiration of these micro-organisms was 350 KC/m²/yr. A rough estimation of the portion of this amount which represents the respiration of algae may be obtained by adding three-fourths of the respiration in April when the algae were most active to one-half of the respiration in March, May, June and July; this gives 55 KC/m²/yr. The respiration of micro-organisms was lowest in April and, since the algae were most active then, most of this respiration must have been due to algae. Since the algae were also active in the four other months mentioned, they must have accounted for a considerable portion of the respiration then as well.

Micro-organism metabolism throughout the year was compared with the various sources of energy upon which these organisms could have drawn. Fig. 5 gives a picture of relative rates of photosynthesis in the spring and respiration of micro-organisms and the energy available to micro-organisms from animal sources (non-predatory mortality and prey killed but not assimilated by carnivores; the chitin in cast larval and pupal skins was not included). It is apparent from the figure that the respiration of micro-organisms is much more closely correlated with the variation in usable energy lost by the macrofauna. This would indicate that the micro-organisms were probably mostly bacteria and fungi and not algae-eating animals.

The nematodes and protozoa, although not abundant, were the only other micro-organisms observed with any frequency. They probably fed mostly upon bacteria. The two genera of nematodes identified had only bacteria in their guts and members of these

genera are reported to feed only upon bacteria (Nielsen 1949).

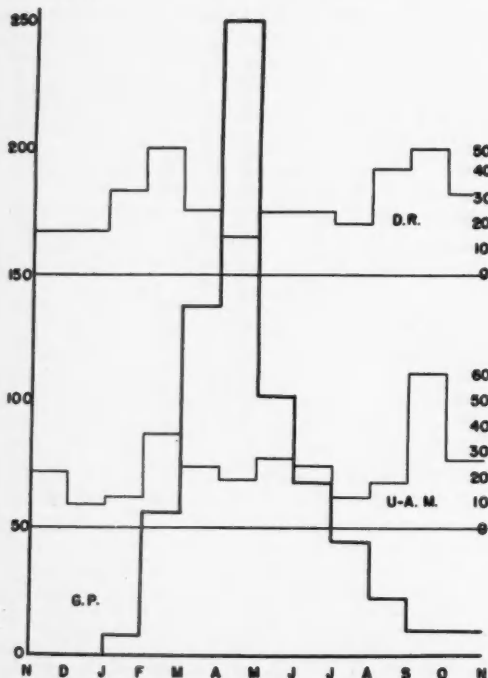


FIG. 5. Comparison of Gross Photosynthesis (G.P.); Mortality of macroscopic animals which is not assimilated by macroscopic carnivores (Unassimilated Mortality, U.A.M.); and Respiration of all micro-organisms (D.R.) for Root Spring, Concord, Mass. in 1953-54.

PHOTOSYNTHESIS

The amount of photosynthesis occurring in the spring was negligible in November and December and very slight throughout the autumn and in January, due to lack of light at those times. It was not until February that the duration and strength of the illumination became sufficient for a large crop of algae to grow in the spring. In February all of the solid surfaces in the water became covered by the filamentous green alga *Stigeoclonium*. This alga increased in amount and a seam of diatoms became visible to the naked eye on the surface of the sandy part of the bottom as the illumination increased. The occurrence of maximum photosynthesis of the algae in April (Table 8) is explained by the fact that after April the terrestrial plants around the spring leafed out and shaded the water. By summer this shading greatly reduced photosynthesis.

The gross production of the algae was 710 KC/m²/yr and since the algal respiration was estimated at 55 KC, net algal production was approximately 655 KC/m²/yr.

A possible source of error in these values lay in the fact that the measurements extended over 24 to 32 hours. It is possible that in this time the available

phosphate or some other essential nutrient was exhausted and that the measured rate of photosynthesis was lower than the true value. However, one experiment in May was allowed to run for five days while another ran only one day in the same week and there was no significant difference in the results. Perhaps these algae are able to use organic phosphate for their growth as Rice (1949) reported for *Chlorella* but failed to find for *Nitzschia*.

BACTERIAL GROWTH ON GLASS PLATES

The numbers of bacteria which grew on the exposed parts of glass slides stuck in the middle of Root Spring allow a rough comparison to be made with other aquatic areas. One slide in the spring for 20 days showed a growth of 625 bacteria/mm²/day (21 fields counted). Two others in the water for 30 days showed 847 and 1070 bacteria/mm²/day (45 and 56 fields counted). Slides placed in a pond into which the springbrook flowed but where the water temperature was about 25° C showed more growth in the pond in two weeks than occurred in the spring in a month.

Comparison may be made with Silver Springs, Florida (Odum 1957) where slide counts at the mud surface gave 3280 bacteria/mm²/day, about three times the Root Spring value. Since Silver Springs has a temperature of 23° C, it would be expected that growth there would be two to three times as fast as in Root Spring with a temperature of 9° C.

Probably some of the bacteria in Root Spring were photosynthetic but the slides were not examined for colored forms. Henriei (1939) indicates that photosynthetic bacteria are more common in shallow water than elsewhere and all of the slides in the spring were in full daylight.

Since respiration of the bacteria is included with that of the micro-organisms and their importance to the community metabolism thus evaluated, they were not considered further.

PREDATOR-PREY BALANCE

From the data for *Anatopynia* and *Phagocata* the amount of energy assimilated by carnivores each month can be found. However, a larger biomass of prey is killed than is assimilated. It has been seen that *Anatopynia* assimilated only about one-third of the amount that it kills and that *Phagocata* assimilated about 90% of its food on the average, as 10% is indigestible. Table 9 lists under "Predation" the biomass of killed prey, given in energy terms, needed to support the carnivores.

The mortalities from all causes of the various prey species are added in the first column of Table 9. *Anatopynia* and *Phagocata* are not included as prey, even though they did feed on members of their own species, because cannibalism has already been taken into account in the energy flow balances.

By comparing the total mortality of the herbivores with the predation it can be seen that for the trophic level as a whole the non-predatory mortality is 19.4%

TABLE 9. Comparison of herbivore mortality and loss due to predation (KC/m²) in Root Spring, Concord, Mass.

Month	Mortality	Predation	Difference Non-pred. mortality
November 1953.....	24.0	16.8	7.2
December.....	21.4	20.6	0.8
January 1954.....	39.4	37.1	2.3
February.....	63.0	51.5	11.5
March.....	32.9	22.1	10.8
April.....	20.8	16.3	4.5
May.....	33.2	29.6	3.6
June.....	32.7	22.7	10.0
July.....	23.1	22.9	0.2
August.....	53.8	54.1	-0.3
September.....	93.8	58.7	35.1
October.....	29.8	24.6	5.2
	467.9	377.0	90.9

of the total mortality $\left(\frac{90.9}{467.9}\right)$

It seems logical to believe that non-predatory mortality would have been smaller in the spring than in other aquatic or terrestrial soils since the constant environmental conditions would result in fewer non-predatory deaths in the spring than would be the case in environments subject to freezing, anaerobiosis, etc.

It may be concluded, then, that non-predatory mortality will be one-fifth or more of the total mortality of a species or trophic level in many communities. It is not, therefore, safe to neglect this part of the energy flow through a trophic level as was done by Lindeman (1942).

RELATIVE IMPORTANCE OF VARIOUS SPECIES

An energy balance sheet for the herbivores and carnivores is given in Table 10. From this table we can compare the various groups of herbivores with respect to the amount of energy which they assimilated and the amount of energy which they transformed to heat. The oligochaetes assimilated more energy than any other group and transformed more than any other group with the exception of the isopods. The Calopsectra, which had by far the largest biomass in the summer, were third in importance in amount of energy assimilated and transformed.

These data emphasize the difficulty in making valid comparisons of the metabolic importance of various kinds of animals from subjective impressions, counts or measurements of biomass, or even energy flow determinations if these are confined to only one season. Statements of the relative importance of various kinds of animals to a community have, however, often been based on just such evidence as individual size and apparent abundance at one time of year. Indeed, the entire scheme of classifying animals as major and minor influents in a community (Clements & Shelford 1939) seems based mostly on the in-

TABLE 10. Balance sheet for herbivores and carnivores in Root Spring, Concord, Mass., 1953-54. Data for Anaptynia are divided between both trophic levels as explained in the text.

	Assimilation	Respiration
Herbivores	KC/m ² /yr.	KC/m ² /yr.
Limnodrilus.....	644	484
Asellus.....	604	486
Calopsectra.....	520	390
Anaptynia.....	159	138
Pisidium.....	173	91
Trichoptera larvae.....	88	67
Physa & Crangonyx...	120	90
Total Herbivores....	2300	1746
Carnivores		
Phagocata.....	131	19
Anaptynia.....	77	70
Total Carnivores....	208	89

adequate criterion of individual size. The use of size as a criterion of community importance has been criticized by E. P. Odum (1953) who suggests that total biomass of a species is a better indicator of the importance of various animals in a community. An even better notion of the relative influence of different populations in an ecosystem is obtained from a study of energy flow.

The planarians were the most important carnivores even though they transformed less energy than the Anaptynia because the latter obtained more energy from plant than animal sources.

By combining all of the data so far presented, the community energy balance chart (Fig. 6) was constructed.

On the credit side of the energy balance is:

Organic debris	2350 KC/m ² /yr (76.1%)
Gross photosynthetic production	710 (23.0%)
Immigration of caddis larvae	18 (0.6%)
Decrease in standing crop	8 (0.3%)
	3086

This total is divided in the following way on the debit side of the balance:

Transformation to heat	2185 KC/m ² /yr (71%)
Deposition	868 (28%)
Emigration of adult insects	33 (1%)
	3086

PORTION OF ENERGY TRANSFORMED TO HEAT

The fraction of assimilated energy which various groups of animals in Root Spring transformed to heat during the year studied is summarized in Table 11. The fraction is close to 50% for all groups ex-

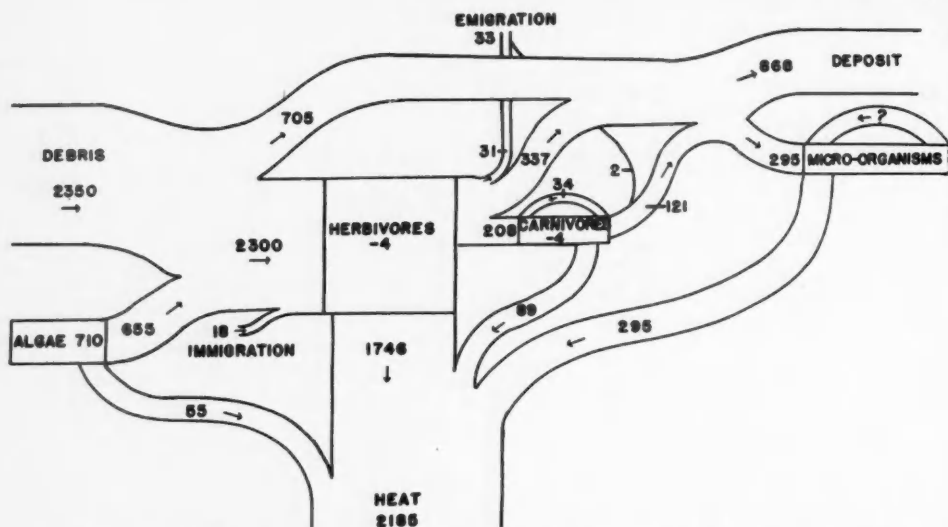


FIG. 6. Energy flow diagram for Root Spring, Concord, Mass. in 1953-54. Figures in $\text{KC}/\text{m}^2/\text{yr}$; numbers inside boxes indicate changes in standing crops; arrows indicate direction of flow.

cept the clams and planarians. (The value for carnivores is low because of the influence of the planarians.)

TABLE 11. Energy ratios for various groups of organisms from Root Spring and from other sources. Efficiencies for *Mytilus* were calculated for season of maximum growth and would be lower if figures on an annual basis as were Root Spring data.

	Net Production Assimilation	Transformed to Heat Assimilation
Root Spring		
Calopsectra.....	20%	80%
Anatopynia.....	13	84
Limnodrilus.....	26	74
Asellus.....	20	80
Trichoptera larvae.....	36	64
Pisidium.....	47	53
Planarians.....	87	12
All herbivores.....	25	75
All carnivores.....	59	37
Entire Community.....	29	71
Jorgensen (1952)		
Veligers, marine.....	60 - 70	..
<i>Mytilus</i> , 40.9-49.0mm....	54	..
<i>Mytilus</i> , 90mm.....	11	..
Harvey (1950)		
Calanus.....	70	..
Brody (1945)		
Embryos.....	50 - 65	..

It was suggested that the reason for the very low ratio of energy transformation in the planarians is their necessity, in an evolutionary sense, to compensate for their large loss of energy in the form of mucus. However, since the energy in mucus serves

the worms in their activities and is subsequently lost to them just as the energy used for doing work and transformed to heat is used and lost, the energy in mucus may logically be included with the energy transformed to heat in calculating the ratio. The portion of energy transformed plus mucus energy was 69% which is comparable to the value for the other animals. The relatively low transforming ratio of the clams may possibly have a similar explanation since these animals lose considerable mucus in their pseudofeces.

EFFICIENCY OF NET PRODUCTION

The efficiency of net production (Table 11) varied around 30% for the animals in the spring except for the clams and planarians with efficiencies of 47% and 87% respectively. These latter two values are close to those for larval animals and embryos while values from 20-30% are more common for efficiencies of post natal growth (Jørgensen 1952). It is possible that the high efficiency in the planarians is associated with their exceptional regenerative ability.

The net production efficiency for the entire community was 29%. In other words, there would be a continual accumulation of usable energy in the ecosystem if organic matter were not removed.

A small amount of organic matter was removed in the bodies of the insects that emerged, 33 KC/m^2 , in comparison to the deposition of 868 KC/m^2 . The pool was prevented from filling completely by shifts in the position of the boils which stir up and wash out some mud.

COMPARISON WITH DIFFERENT COMMUNITIES

With the data available in the literature comparisons can be made, not only of the primary produc-

tivity in a series of communities but also of the energy flow through the trophic levels of a much smaller number of systems.

Table 12 gives values for energy available to organisms other than primary producers (primary net production plus accumulated energy in organic matter) and the ratio of this to total incident light. Incident light in the Concord region was calculated to be 1.095×10^6 KC/m²/yr from weather bureau data (U.S. Dept. of Commerce 1951). In aquatic communities some light is absorbed by the water but in order to make comparisons between land and water systems as producers on the earth, no correction was made.

TABLE 12. Efficiencies and productivities of various communities compared with those of Root Spring, Concord, Mass.

	Energy available to consumers	Column One Light	Gross Prod. Light	Source
	KC/m ² /yr.			
Root Spring.....	3005	0.27%	0.2%*	
Eniwetok Reef.....	21800	1.8	5.8	Odum & Odum 1955
Cedar Bog Lake.....	879	0.074	0.1	Lindeman 1942
Lake Mendota**.....	3730	0.31	0.4	Lindeman 1942
Minnesota Pond.....	394	0.033	0.04	Dineen 1953
Corn field in summer	6170	1.2	1.6	Transeau 1926
Georges Bank.....			0.3	Clarke 1946
Silver Spring, Florida			8.0	Odum 1957
Average Terrestrial plant.....			0.09	Riley 1944
"Best forests".....			0.25	Riley 1944

*For April only.

**Values considered erroneously high by Lindeman.

Root Spring provided more energy per unit area for consumers than average temperate communities because of its action in accumulating energy that had been fixed by plants outside of the spring. The spring community itself expended no energy to bring about this accumulation.

As far as primary gross production is concerned, the algae of Root Spring were as efficient as the better temperate communities. The efficiency was calculated for April before shading by trees was important, since no direct measurement of light intensity was made.

Comparisons of the different trophic levels of a few communities are made in Table 13. The ratio, $\frac{\text{assimilation of one trophic level}}{\text{net production of next lower level}}$, is used for comparison. This represents the efficiency of utilization of available food by a trophic level. Values were calculated from the data given by the various authors.

The most striking difference shown in Table 13 between the various communities is the large assimilation and efficiency of herbivores in Root Spring. (The large carnivore assimilation appears to be a result of the large food supply in the form of herbivores since the efficiency of carnivores in Root Spring was about the same as in the other communities.)

The reason that a large portion of the available plant energy was assimilated probably lies in the fact that the Root Spring conditions were more favorable to life than those in the other environments of Table 13. For example, water currents in the spring provided sufficient oxygen and rapid removal of metabolic wastes at all times. It must be noted, however, that the transformation by a community of as much or more than three-fourths of the incoming usable energy to heat is not unusual.

If in any community the primary net production is not accumulating to any appreciable extent, as is the case in the woods in the south of England (Pearsall 1948), it is because the efficiency of utilization of primary net production is close to 100%. In other words, if the primary consumers consume all the primary net production there will be no accumulation of organic matter in the community. This contradicts Lindeman's (1942) thesis that the utilization efficiency will be progressively greater for higher trophic levels.

In Root Spring the primary consumers are mostly macroscopic animals. These animals are herbivores, detritus feeders, and scavengers. In terrestrial soils, on the other hand, the most important primary consumers are probably microscopic, heterotrophic plants. Data summarized from Stöckli (1946) indicate that the microflora—fungi, bacteria, actinomycetes (and algae)—compose most of the biomass of terrestrial soil organisms, and since these organisms are also very small, they are undoubtedly the most active metabolically. These plants are "decomposers," but are still primary consumers as long as they are burning fuel from green plant sources. It makes no difference in an energy flow analysis, whether organisms which obtain energy from plants are herbivores, saprophytes, detritus feeders or decomposers; they are still all primary consumers.

A complicating factor arises from the fact that decomposers, etc. feed upon consumers as well as producers (i.e. are secondary and tertiary as well as primary consumers). This complication is common to all soil communities, aquatic and terrestrial, and does not invalidate the comparisons made from Table 13.

The data from this investigation raise a number of interesting questions: Is it a general rule that the ratio of energy flow of secondary consumers to that of primary consumers remains about the same for all communities? Does the stability of a community affect the aforementioned ratio? What relation might there be between assimilation by primary consumers and producer net production? Is there a correlation between body size of consumers and deposit or removal of a sizable fraction of primary net production? These and other questions can only be answered when more data from both experimental and natural communities are available.

SUMMARY

1. A study of community metabolism in terms of energy flow was undertaken in 1953-54 in order to

TABLE 13. Efficiencies and assimilations for higher trophic levels of various communities compared with those of Root Spring, Concord, Mass.

	ROOT SPRING		CEDAR BOG LAKE		LAKE MENDOTA		MINNESOTA POND		SILVER SPRING
	Assim.*	Effic.**	Lindeman (1942) Assim.	Effic.	Lindeman (1942) Assim.	Effic.	Dineen (1953) Assim.	Effic.	Odum 1957 Assim.
Primary Consumers (Herbivores)....	2300	76%	148	16.8%	416	11.2%	92	23%	1280
Secondary Consumers (Carnivores)....	208	36%	31	29.8%	23	8.7%	34	47%	28
Tertiary Consumers (Secondary Carnivores)....	3	23.0%

*All assimilations are KC/m²yr.

Assimilation

**All efficiencies are

Net production of next lower trophic level

provide a more accurate picture of energy flow through the populations of a community than had hitherto been available. Root Spring, a temperate cold spring in Concord, Massachusetts, was chosen for study because of the relatively constant environmental conditions and simple biota.

2. The energy flow through the larger animal populations was studied in detail. These animals included two chironomids, *Calopsectra dives* and *Anatopynia dyari*, a tubificid oligochaete, an isopod, two planarian species, three species of caddis larvae, two species of fingernail clams, one snail, and one amphipod. To minimize artificial disturbance of the community the animals in the samples were kept alive and returned to the spring after being weighed and counted.

3. Respiration of the larger species of animals was measured in containers filled with spring water and placed in the spring so that conditions were as nearly natural as possible. Photosynthesis and respiration of the micro-organisms were determined by measuring oxygen changes in water over bottom mud enclosed in light and dark, covered glass cylinders.

4. Non-predatory mortality was calculated as the difference between the total mortality determined with the formulae published by Ricker (1946) and the mortality due to predation. Non-predatory mortality accounted for nearly 20% of the mortality occurring in the herbivore trophic level. Reasons were given for believing that this was a lower rate of non-predatory mortality than exists in most communities and that non-predatory mortality may not be safely neglected in studies of productivity.

5. The *Anatopynia* were found to assimilate only 30% of the prey which they killed. This carnivorous midge larva actually obtained about two-thirds of its food from plant sources which enabled it to exist during periods in which it could not obtain sufficient animal food.

6. Phagocata, the planarian, lost more energy in the mucus which it secreted than it used in doing external and internal work as measured by respira-

tion. Mucus secretion took 79% of this species' net production.

7. 76% of the energy transformed by the organisms entered the spring in leaves, fruit and branches of terrestrial vegetation. Photosynthesis in the spring accounted for 23% and less than 1% entered in the bodies of immigrating caddis larvae.

8. The micro-organisms respired about 350 KC/m²/yr. Of this only 55 KC were respired by algae, the remainder by bacteria, fungi, protozoa and nematodes. Evidence was given to indicate that most of the micro-organisms were feeding upon animal remains.

9. The most conspicuous group of herbivores, *Calopsectra*, was only third in importance in energy flow. It was suggested that the relative amount of energy which flows through each population is a better criterion than size or biomass of the importance of various animal species in a community.

10. The energy balance sheet for the community shows that, of the year's total energy input, 71% was transformed to heat, 28% was deposited in the community and only 1% emerged in adult insects.

11. The efficiency of energy transformation, energy used for internal and external work as measured by respiration divided by assimilation, was close to 80% for all animals but the planarians and clams. The clams transformed only 53% of their assimilation, the planarians only 12%. These low rates of respiration may be an adaptation connected with the large amounts of mucus lost by these animals.

12. The ratio $\frac{\text{assimilation}}{\text{net production of algae plus energy of organic debris}}$

was 76% in Root Spring, higher than other aquatic communities investigated but probably not as high as for some soils.

13. The efficiency $\frac{\text{algal photosynthesis}}{\text{available solar energy}}$ in Root Spring in April when shading of the water at a

minimum was 0.2% which is comparable to any temperate area. If the efficiency of the spring community is calculated on the basis of total inflow of energy instead of just photosynthesis, the efficiency for the year was 0.27%, higher than for most temperate latitude communities which have been studied.

14. The assimilation by macroscopic primary consumers (over 1 mg) was five times that reported for any other temperate latitude aquatic community. The steady flow of constant temperature water bringing oxygen, removing waste, and enabling the animals to be active all year was probably responsible for this high assimilation.

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REACTIONS OF *ANOPHELES QUADRIMACULATUS* SAY TO MOISTURE, TEMPERATURE, AND LIGHT

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INTRODUCTION

The objectives of this investigation are: (1) to elucidate basic knowledge about insects and particularly adult anophelines; (2) to determine the reactions of the experimental organism to temperature, moisture, and light, separately and in various combinations; (3) to use these data in establishing base lines against which field studies may be evaluated; (4) to develop criteria, methods and techniques for these laboratory studies; and (5) to evaluate the ecological and genetical implications of such procedures.

The studies, carried out from May, 1954, to June, 1956, constitute the third of three major aspects of a comprehensive research program concerned with adult mosquito behavior. These three aspects are: (1) field studies which are based on precise and continuous measurement of the major environmental factors through several years' time, vertically from sub-surface to tree-crown zone and horizontally through various community types from points of greatest to points of low or zero population density;

(2) the collection and evaluation of comparable distributional data of adult mosquitoes in space and time; (3) the carrying from the field to the laboratory of problems requiring laboratory analyses where experimental techniques can be applied. Only with these kinds of data in hand is there a reasonable expectation for understanding the critical conditions or combination of conditions operating to control given mosquito or other insect populations in nature.

Although this is the first report on the laboratory aspects of the program, several reports have been published on the field aspects. All of the field work has been carried out in a special experimental area at the Emory University Field Station, located in the Upper Coastal Plain of southwest Georgia. Platt (1955) reported on the general program, particularly with regard to the facilities available for field work. An analysis of the microenvironmental data obtained for this area for the first two years of operation has been made by Platt & Goodwin (unpublished). Another paper (Platt 1957) gives a detailed account of the far more accurate field instruments subsequently installed for determining and recording environmental data.

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THE EXPERIMENTAL ORGANISM

The malaria mosquito, *Anopheles quadrimaculatus* Say, has been selected as an experimental organism because it is a species which is also being studied at our field laboratory, is already well known, and has a wide distribution; also, laboratory strains can be easily reared from eggs.

Although wild-caught individuals of this species usually will not breed in captivity, several strains have been isolated from natural populations.

The laboratory strain used throughout this study, with two minor exceptions, was originated about 1930 and maintained by techniques described by Bradley, Goodwin & Stone (1949). The eggs were obtained from the insectary at the Emory University Field Station. The two exceptions, which refer to one temperature and one light experiment, were necessitated by unavailability of eggs from the Field Station toward the close of the experimental work. Another strain was used for these two experiments which had been isolated in 1944 and continuously maintained since that time by the Technical Development Laboratories, U. S. Public Health Service, Savannah, Ga. (Schoof, pers. comm., 1955).

Summaries of mosquitoes used are presented in Table 1. These figures are conservative, and do not include numerous preliminary experiments which were requisite to the establishment of techniques and procedures. For the entire series of experiments approximately 200 lots of 30 mosquitoes each, a grand total of 6,040 individuals, were used. A total of 56,790 individual observations were recorded for these,

since, in most experiments, each mosquito was observed several times.

TABLE 1. Summaries of Mosquitoes used.

	Number of individuals (used in lots of 30 each)	Total number observations
I. REACTION TO ATMOSPHERIC MOISTURE		
A. Gradients	1,050	3,150
B. Desiccation	660	8,040
II. REACTION TO TEMPERATURE		
A. Rising	180	2,160
B. Constant	1,680	16,800
C. Effects of age and feeding	360	3,600
D. Recovery	180	1,260
III. REACTION TO RADIANT ENERGY		
A. Intensities	300	1,800
B. Colored lamps	360	5,400
C. Bourges filters	540	2,340
D. Monochromatic filters ..	420	3,240
E. Color temperatures	300	9,000
GRAND TOTALS	6,030	56,790

LITERATURE REVIEW

The literature on *A. quadrimaculatus* has recently been brought together by Horsfall (1955). This, as well as other reviews by Bates (1949) and Thomson (1951), shows that studies on anopheline mosquitoes have been concentrated on tropical species, primarily because these include the most important malaria vectors. Thus the literature on *A. quadrimaculatus* is relatively scanty. The few papers concerned with the ecology of the adult stage have dealt variously with local distribution, resting places, diurnal movements, dispersal flight and ranges, feeding, ovulation, oviposition, and longevity.

According to Horsfall (1955), *A. quadrimaculatus* is restricted to eastern North America, roughly from southern Ontario throughout the United States east of a line from Minnesota south through central Texas. The season of abundance ranges from approximately four months in the northern part to about eight months in the southern part of the range. Generations vary, likewise, from 2 or 3 in the North to 8 or more in the South, individual longevity varying usually from 2 to 5 weeks. Flight studies indicate an average effective range of perhaps a mile, although flight distances up to two miles have been frequently observed. The species is primarily a pond and swamp breeder and is frequently associated with certain vegetation types. Adults are normally found in secluded resting places during the day, leaving them about dusk and returning to the same or different resting places early the following morning. In general, resting places have been observed to be noticeably cooler, moister, and darker than adjacent areas. Conse-

quently, tree-holes, boxes, sheds, barns, houses, and other such areas offer excellent sites. Obviously, in order to encourage continuous use, the sites must also be near to a dependable source of blood and to an oviposition site.

Many field studies have been carried out on responses of adult mosquitoes to atmospheric moisture, but few have been conducted in the laboratory where humidity and temperature conditions could be controlled and especially where the population has been used as the unit of study. The more critical laboratory studies on humidity effects have been those in which gradients were utilized. In such experiments with *Anopheles maculipennis* and *Aedes aegypti*, Martini & Teubner (1933) found that both species showed a general preference for higher humidities, although this reaction was not always sharp. A pattern consisting of high humidity preference up to a point, indifference, and then low humidity preference was reported by Rudolfs (1923, 1925) for *Aedes sollicitans*, *A. cantator*, and *Culex pipiens*, and by Thomson (1938) for *Culex fatigans*. Differences indicated for optimum humidities evidently depended partly upon the species involved. In studies using an olfactometer, Brown, Sarkaria & Thompson (1951) found that moist air at 85% relative humidity attracted three to five times as many *Aedes aegypti* as dry air at 15%. Lewis (1933) concluded from experiments on *Aedes aegypti* that the length of life of fed and unfed mosquitoes at 23° C is dependent on humidity but is not directly related to saturation deficiency.

The only available studies on the relationship of mosquito behavior to rising temperatures are those by Rudolfs (1923) and Thomson (1951), although detailed studies have been made on other insects, such as that by Nicholson (1934) on blowflies. Thomson exposed *Anopheles minimus* females to temperature increases at the rate of 5° C per hour. He found a peak of activity at 36° with most of the mosquitoes in flight. With further increase, the mosquitoes became inactive, and between 37° and 38° C the majority died after an exposure of 5 or 10 minutes. This fatal temperature zone remained the same over a wide range of humidity conditions from 25 to 95% R. H. Newly emerged unfed females and freshly engorged females were equally susceptible to the effects of high temperature. Thomson also found that *Anopheles vagus*, with a thermal death point between 40° and 41° C, was more resistant to high temperatures than *A. minimus*.

Comparatively few studies have been made with regard to the influence of high temperatures on the reactions of insects in general, and only three were found which had been done on adult mosquitoes in particular (Martini & Teubner 1933, Mellanby 1934, and Thomson 1938). The results of these are in agreement with results obtained in the experiments referred to above on rising temperature. The experiments of Thomson (1938) and of Martini & Teubner (1933) were primarily concerned with temperature prefer-

ences which the mosquitoes manifested when given an either-or choice in a temperature gradient having a 5° to 17° C range. Thomson exposed *Culex fatigans* females in various physiological states to a range of 5° C at different parts of the temperature scale and found that their sensitivity was much greater at high temperatures (25-30° C) than at low ones, the mosquitoes being sensitive to a choice of only 1° C. Mellanby found that with exposures of 1 and 24 hours' duration approximately 75% of both the unfed and gorged adults were able to survive at 39° C for 1 hour but that all were killed at 40° C. Full-fed mosquitoes survived 37° C for 24 hours in moist air (90% R.H.) but not more than 32° C in dry air (0% R.H.). Mellanby's work lacks definiteness in that only approximate survival values are used and the times of individual "knockdowns" are not recorded. Lethal temperatures depend on length of exposure, atmospheric humidity, and age and physiological state of individual mosquitoes. Furthermore, temperature effects cannot always be easily separated from humidity effects. Some additional papers primarily concerned with this are by Bacot & Martin (1924), Beattie (1928), Mellanby (1932), Ramsay (1935a, 1935b), and Johnson (1942).

Few studies have been published on the phototactic responses (i.e., directed movements) of *A. quadrimaculatus* to light, and none of these has been carried out in the laboratory. In fact, relatively few critical phototactic studies have been conducted with any species of mosquito, most of the work with insects being done with other groups. Recent reviews of the literature have been given by Weiss (1943), Andre-wartha & Birch (1954) and Thomson (1951).

Love & Smith (1957) conducted a series of field studies in which light traps were compared with mechanical sweep nets. In these studies *A. quadrimaculatus* demonstrated a definite avoidance of light, since much larger numbers in every case were caught in the nets. Light trap studies by Headlee (1937), Johnson (1938), Carnahan (1939), and MacCreary (1939) confirm this observation. Field experiments designed to test the relative attractiveness of transmitted light of different wave lengths also yielded negative results for the same reason. The only wave length attraction study found involving *A. quadrimaculatus* is that by Goodwin (1942) in which the species was offered, in its natural habitat, a series of colored artificial resting boxes. He found that they alighted in the largest numbers in red boxes, although others were freely used.

Other papers of particular interest regarding light are by Brett (1938), Brighenti (1930), Gjullin (1947), Hundertmark (1938), Ko (1925), deMeillon (1937), Seguy (1938), and Brown (1954).

MATERIALS AND METHODS

Basic experimental methods are presented here. Additional details are given with descriptions of particular experiments. The primary principle underlying these studies is that of attempting to simulate

in the laboratory natural conditions which the experimental organism encounters in its native habitat. Accordingly, these four methodological criteria been established: (1) use of a multiple rather than a single factor approach, (2) use of intensity gradients comparable to those obtaining in nature, (3) use of the entire population as the experimental unit, and (4) use of experimental organisms of known age, sex, and physiological state.

REARING TECHNIQUES

All mosquitoes used in this study were reared from weekly shipments of eggs. Using standard techniques described by Bradley, Goodwin & Stone (1949), eggs were placed on tap water in rearing pans in an insectary. Larvae were fed finely ground dog biscuit until pupation. Adults emerged into lantern globe type cages, where they were stored and fed a 10% glucose-water solution placed on cotton pads. The physical environment was controlled to permit normal development of all stages in the life cycle, temperatures in the insectary ranging from 21-26° C and humidities from 70-75% R.H. The total period of development from egg to adult ranged from 14 to 21 days.

The male and female mosquitoes used for experimentation were obtained from the insectary at known ages and nutritional states. Removal of the mosquitoes from the globe cages and segregation by sexes was facilitated by slight anesthetization with Merck U.S.P. ether. Observations by Willis & Roth (1952), repeated by us, indicated no appreciable differences between the responses of previously anesthetized and non-anesthetized mosquitoes. In no case were mosquitoes under anesthesia introduced into the experimental chamber. Rather, they were allowed to recuperate and then introduced by use of an aspirator type collecting tube so that responses could be immediately observed.

THE EXPERIMENTAL CHAMBER

In accordance with the basic criteria stated above, a multiple factor environmental gradient control chamber was designed and built. This chamber is a plastic tube 137 cm long and 10 cm in diameter, surrounded by separate water baths lengthwise and at either end for temperature control (Figs. 1 and 2). All inflow and outflow pipes are located on either end for control of water circulation. Solution boxes for relative humidity control are at either end, and an entrance door is located in the top center. Nine 6 mm diameter openings spread evenly lengthwise across the top permit the insertion of sensing elements for determination of temperature and humidity along the length of the chamber. This whole structure is located in a light-tight box 190 cm long, 90 cm high and 50 cm deep, in which appropriate light fixtures operated by external switches are installed at either end and above.

This chamber provides for the establishment of the simultaneous production of environmental gradients or constants of relative humidity, of temperature, and of wave length, color temperature, and intensity

of light. Although only a selected few of the possible combinations have been used, the potential number is very large. For example, if the numbers of variations developed for each of these factors are multiplied by each other, more than 10,000 combinations of environmental conditions can be established.

Throughout this series of studies efforts were made continuously to keep the test chamber and housing as clean and free from odors as possible.

TEMPERATURE

All temperatures within the experimental chamber were controlled by circulating water of known temperature through the water bath surrounding the chamber lengthwise and the two separate water baths at either end. Temperature gradients were established by circulating water of different temperatures through the two end baths, these being higher and lower, respectively, than that being circulated through the lengthwise chamber. The maximum temperature gradient established by this means at ambient temperatures was 5° C. For experimental programs calling for constant temperatures, a water bath equipped with an Amineco regulator with a sensitivity of $\pm 0.01^\circ$ F, employing heating elements of 1500 watts, and a $\frac{1}{2}$ h.p. refrigerating unit operating in a three gallon constant temperature bath was utilized. When different temperatures were required for each of the three water baths of the chamber, Model 3L71 Barnes water pumps were used to supply water from various constant temperature reservoirs. The rate of flow varied from 1000 to 1400 cc per minute, which was adequate to maintain a constant temperature throughout the length of the chamber at temperatures from 15° to 40° C. However, at higher temperatures the heat loss along the length of the tube was such as to cause a gradient of as much as 6° C along the length of the chamber. All ambient temperatures within the chamber were measured by inserting mercury bulb thermometers (-10° to 110° C) along the nine sensing element openings along the top of the chamber. By regulating the depth to which these were inserted, micro-temperature gradients within the chamber at very high and very low temperatures could be detected. Such micro-gradients enhanced the use of the chamber. All thermometers were calibrated against a standard and temperatures were usually read to the nearest 0.5° C.

HUMIDITY

Atmospheric moisture within the chamber was controlled by the use of glycerol-water solutions placed in the boxes at either end of the chamber, the techniques employed being those described by Johnson (1940). Within our experience glycerol-water solutions were preferable to salt solutions because they maintained the desired humidity over a longer period of time and were easier to manipulate. Only distilled water and Merck's C.P. glycerin were used. However, when completely dry air was desired, calcium chloride crystals were used. Gradients of 5 to 15% spread within the range of 40 to 95% R. H. were

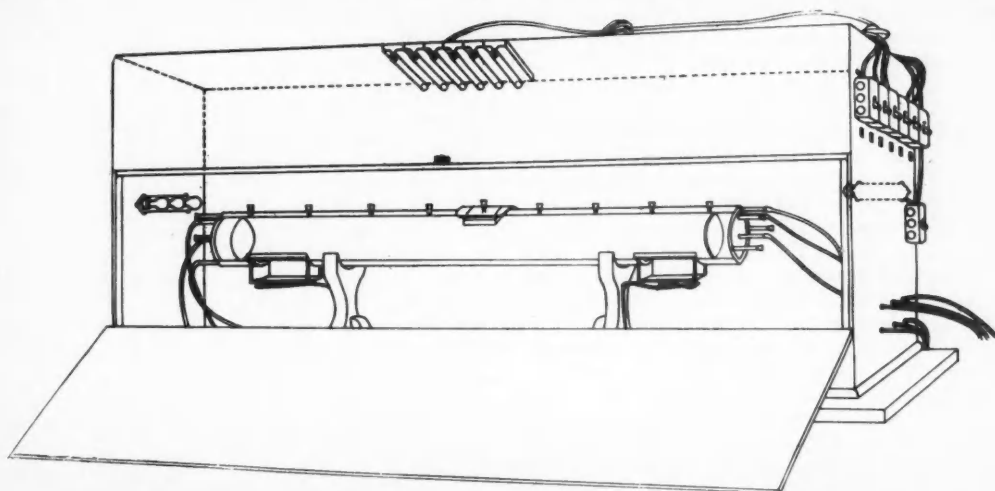


FIG. 1. Diagram of the multiple factor environmental gradient control chamber. The chamber is shown through the open door of the light-tight box.

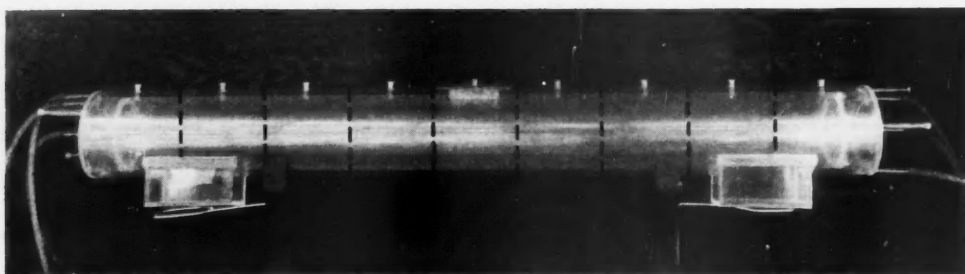


FIG. 2. Closeup of the experimental chamber. Vertical dotted lines superimposed on the photograph indicate the nine positions used for distribution analysis.

easily established. Gradients up to 20% could be maintained for short periods of time. Constant humidities from 0 to 80% were similarly established. The relative humidity measurements were translated into absolute moisture and into vapor pressure readings where indicated. Determinations of moisture were obtained along each gradient by insertion into the chamber of a direct reading Model 201 Serdex relative humidity meter having a $\pm 1.5\%$ accuracy. By slowly moving the meter along the length of the chamber on a trolley wire provided for this purpose, gradients were triple-checked against various combinations of glycerol-water solutions at given temperatures. This enabled the meter to be removed when the mosquitoes were utilizing the chamber, thus eliminating it as a possible extraneous factor in affecting their behavior. Moisture determinations were also made by using an "Alnor" type 7000U No. 1142 dew-pointer having an error of less than 1% and utilizing only 300 cc of air per determination.

The regulation and determination of relative humidity proved to be the most difficult technical task encountered. This was in spite of the fact that the rela-

tive humidity of the atmosphere over a glycerin solution, according to Raoult's Law, is essentially independent of temperature. Most difficulties arose from the fact that the time required to reach an equilibrium varies with the temperature, the volume of the air, and the surface area of the solution. In the majority of experiments it was undesirable to measure the relative humidity with the organisms present. Therefore, the customary procedure has been to set up the conditions indicated and usually to make two or three dry runs for the specific purpose of obtaining time versus relative humidity data. In the case of humidity gradients, where an effective gradient may not be maintained for more than a few minutes, three separate checks were made for each gradient used.

WAVE LENGTH AND INTENSITY OF LIGHT

The wave length and intensity of light was controlled by the use of appropriate incandescent and fluorescent lamps and monochromatic light sources with appropriate filters, when needed, at either end and above the light-tight box in which the experimental chamber was located. All light intensity meas-

urements were made at appropriate places inside the plastic tube with a Model 200 Photovolt unidirectional photometer. The intensity ranges utilized in the tube were from 0.01 to 2,000 foot candles of light.

The wooden box in which the chamber is located was painted a dull black to prevent reflections. With the outer door closed the box is light-tight, one-half inch covered portholes along the front providing for observations without appreciably altering the light distribution, except at low intensities when they are kept closed. In color attraction studies, the only light which the mosquitoes see is that emanating from the lamps located at either end of the box. All intensity determinations have been made within the tube, those reported representing the maximum ones obtained at the center of either end wall. Intensities midway of the tube are less because of the inverse square law. This arrangement permits a mosquito in the center of the tube to face an intensity, for example, of 500 foot candles in one direction, but only a small fraction of a foot candle in the other. Although an either-or type of response is used, the experiments are so arranged as to provide usually a series of small differences, or combination of differences, which approximate conditions obtaining out of doors.

COLOR TEMPERATURES

Color temperatures, i.e., the color of a completely radiating black body source, and of light sources which visually match such a source (expressed in ° Kelvin) were set up in the chamber by the overhead use of appropriate combinations of fluorescent and incandescent lamps (Weitz 1950). Natural out-of-doors light exactly matches certain color temperatures, sunrise equalling a color temperature of 1500° K, 30 minutes after sunrise 2200° K, average noon sun 5300° K, overcast sky 7000° K, blue sky 12000° K, and an extremely blue clear northwest sky 26000° K.

SAMPLING METHODS AND ANALYSES OF RESULTS

In order to provide a method for rapid determination of mosquito distribution within the chamber, it was diagrammatically divided into 9 equal positions (Fig. 2), each having in its center a sensing element opening. The basic experimental design utilized a lot size of 30 individuals. Each experiment was run in triplicate, the position of each of the 30 mosquitoes for each of the three replicates being indicated on a diagram. For each experiment, therefore, a total of 90 observations on 30 individuals was made. This basic design was varied according to the requirements of special experiments. Sometimes the same lot was used for two or more experiments, and in other cases was discarded without replication.

When initially introduced into the chamber, the light-tight box was closed and the mosquitoes were given 5 minutes to make a position preference. Then, either the box or special peep-holes were opened, and the position of each mosquito was recorded according to the 9 basic positions or parts of the chamber. For the second and third replicates the mos-

quitoes were thoroughly stirred with a 2-ft length of thin flexible wire or, in a few experiments, disturbed by slapping the sides of the tube, and the above procedure repeated. A new lot of 30 individuals was used then for each complete experiment, except when it was necessary to continue observations on the same lot, or when conditions permitted continued use of the same lot, as in color preference studies.

In all experiments in which basic procedures were being established, and in the more critical experiments subsequently conducted, the response was double checked as follows. When experimental procedures permitted, the environmental conditions between the ends were reversed without removing the mosquito sample from the tube. In other experiments, the environmental conditions were reversed and a new sample introduced. In temperature studies, the inflow and outflow of water in the jacket of the tube was reversed, thus reversing the gradient.

The experimental control or base line against which responses to varying environmental conditions have been evaluated was established by two distribution studies carried out within the chamber under constant conditions. The first of these was done by introducing, singly, 180 mosquitoes into the chamber under constant conditions of humidity and light. Only one mosquito was in the tube at a time. The position in which each mosquito alighted within one minute was recorded. On this basis 45.5% (82 individuals) alighted in the middle five positions and 26.7% (48 individuals) and 27.8% (50 individuals) in the two right end and two left end positions respectively (Fig. 3). Distribution within the 9 zones indicated that several more mosquitoes were in each of the extreme end positions than in any of the 7 middle positions. This may be due in part to the fact that the end plates provide a greater surface area for the mosquitoes to alight on, and that these plates provide a terminus for flight along the length of the chamber. Since, however, the distribution among the middle 7 positions was normally approximately equal and the numbers in the extreme end positions were also approximately equal, it may be assumed that any statistically significant difference between numbers obtained for either end under experimental conditions is due to mosquito response to the specific conditions present.

The second check on the validity of the above procedures was made by conducting special flight experiments in the chamber, which consisted of introducing singly 50 mosquitoes and timing their flight between 6 successive rests each, 95% of these flights having to be mechanically stimulated. The time from entrance to first alighting of these 50 mosquitoes varied from 2 to 55 seconds, with a mean time of 11.5 seconds. After alighting each mosquito tended to remain stationary unless mechanically agitated. These results indicate that one minute was adequate time for each of these control mosquitoes to alight, and that the 5-min period allowed in the experimental runs is more than adequate for determination of

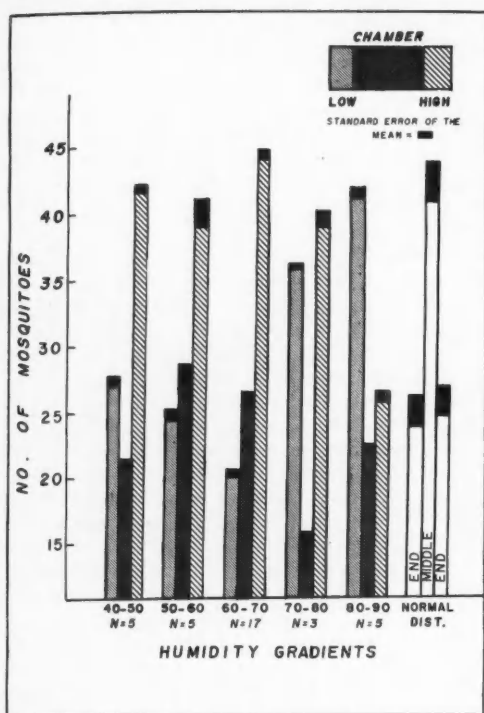


FIG. 3. Distribution of mosquitoes in ten per cent relative humidity gradients, as compared with the normal distribution.

mosquito preference. Furthermore, since mosquitoes tended to remain in the same position after alighting, any additional time allowed does not appear to have any influence on the position after it is once made. Since in experimental cases the conditions are varied rather than constant, the additional 5-min period again seems justified.

It may be pointed out here that the use of a circular chamber would eliminate the obvious disadvantages arising from the end walls of the linear chambers.

For most distribution experiments it was found that 3 rather than 9 zones of the chamber were quite adequate, these zones being composed of the two left end, the middle five, and the two right end positions. Analyses carried out on the basis of other combinations of positions failed to indicate as good a basis for evaluation of results as the 2-5-2 distribution. This method has the added advantage that in relative humidity measurements the two positions on either end and directly over the solution boxes have no gradient of humidity, and should be treated alike. For example, in a chamber gradient of 40-50%, each of the two extreme positions on the low humidity end were measured at 40%, and each of the two on the high humidity end at 50%, the gradient being spread over the middle five positions.

All of the above checks were made with the labora-

tory strain obtained from the Emory University Field Station. They were not repeated with the strain obtained from Savannah, since it was used only for a single experiment on light and one on humidity, and these experiments did not justify the time required. This strain is specified in the particular experiments in which it was used.

In summary, criteria for evaluation of behavior with reference to the normal distribution are: (a) relative balance or imbalance of distribution between the two ends, and (b) total numbers aggregated in the ends as opposed to the middle. The extent of the imbalance would show the intensity of the response in terms of the population, and the direction of the imbalance with reference to the stimulus would indicate a negative or positive response. On the other hand, a balance approximating the "normal" distribution would demonstrate indifference or lack of response. When the distribution is balanced but the total number aggregated in the ends exceeds that of the "normal," an undirected excitation exists, its degree varying with the extent of disproportionateness.

RESULTS

MOISTURE

Responses to relative humidity gradients.—Reactions to increases in relative humidity at 10% gradients from 40 to 90% followed a sigmoid pattern when plotted against numbers of mosquitoes (Fig. 3). A definite preference was shown for the higher humidities in gradients up to 70%, with the greatest preference occurring in the 60-70% gradient. The least preference was shown in the 70-80% gradient, the number of mosquitoes on each end of the chamber being almost equal, with fewer found in the middle five positions than in any other gradient. In gradients above 80% the lower humidities were preferred. More mosquitoes chose the lower humidity in the 80-90% gradient than in any other. When these relative humidity gradients were reversed, the mosquito responses remained approximately the same.

Experiments run at humidity gradients other than the 10% spreads gave results that were practically the same. In 5% gradients, fewer mosquitoes responded to the extremes than in 10% gradients. Steeper relative humidity gradients, of 20% spreads for example, have served as checks on the above results obtained for humidity responses. Thus the optimum relative humidity appears to be between 70 and 80%.

All of these humidity experiments were repeated at 5° C temperature intervals from 15-30° C, in light up to 500 foot candles, and in darkness. In all of these, humidity preferences were independent of the temperature and light conditions used. Details of these particular experiments have been presented by Witherspoon (1954).

Responses to vapor pressure and absolute humidity gradients.—Within the temperature range from 15° to 32° C, the relative humidity rather than the absolute humidity, vapor pressure, or vapor pressure deficit,

has proved to be the critical factor determining mosquito response to atmospheric moisture. It is impossible, of course, for responses to be correlated with relative humidity and also with these other factors. This is illustrated by Table 2, in which equivalent values of these three factors have been calculated from selected relative humidity values at 15° and 32° C. Response to relative humidity is independent of temperature, since at both temperatures the mosquitoes, as demonstrated in previous experiments, exhibit a definite preference for 70% R.H. over both 50% and 90% R.H.

TABLE 2. Relationship of vapor pressure, vapor pressure deficit, and absolute humidity to relative humidity at low and high temperatures. Note that the only factor to which response is independent of temperature is relative humidity, the 70% level being preferred over either the 50% or 90% levels, at both high and low temperatures. The figures show clearly that correlation of behavior with relative humidity precludes correlation with these other factors.

Temperature	Relative humidity	Vapor pressure	Vapor pressure deficit	Absolute humidity
15°C.....	90%	1.5	11.5	12.5
32°C.....	90%	3.0	32.0	36.0
15°C.....	70%	4.0	9.0	10.0
32°C.....	70%	10.0	25.0	27.5
15°C.....	50%	6.5	6.5	7.0
32°C.....	50%	17.5	18.0	19.5

The following example, taken from Table 2, clearly demonstrates these facts. Air at 15° C and 50% R.H. has an absolute humidity of 7.0 mg/liter; at 70%, 10.0; and at 90%, 12.5. The preference is thus shown for an A. H. of 10.0 mg/liter over 7.0 and 12.5 mg/liter, and this pattern could logically be expected to apply at 32° C. Air at 32° C and 50% R.H. has an absolute humidity of 19.5; at 70%, 27.5; and at 90%, 36.0 mg/liter. Since air of 10.0 mg/liter A. H. had previously been preferred to that of 12.5, the lower A. H. should be preferred at this temperature, but instead that of 27.5 mg/liter A. H., corresponding to the relative humidity of 70%, is indicated. The same situation is encountered when both vapor pressure and vapor pressure deficit are considered.

Effects of duration of time on survival in dry air.—Experiments on the effects of duration of time on exposure to various humidities have been divided, for convenience, into short-term exposures and long-term exposures. In all experiments involving short-term (20 minute) exposures to high and low humidities over a wide range of temperatures, the effects of lethal temperatures were primarily independent of humidity, whereas at sub-lethal and ambient temperatures, the duration of time was too short to permit any humidity effects to be manifested. These studies are reported in the section on temperature.

The following series of experiments have been designed to establish the long-term effects of humidity on the populations at room temperature, this being an optimum temperature for survival, as well as one frequently encountered in nature. A total of 660 individuals were used (420 ♀♀, 240 ♂♂ ranging from 3-9 days in age, and fed only on glucose. Results of these experiments, summarized below, are also presented in Figure 4.

Exp. No. 1: Fifty ♀♀ and 41 ♂♂, 2-6 days old, were placed in separate containers at 27-28° C, over calcium chloride crystals. The initial R. H. of 27% dropped to only 20% in 7 hours, and remained at this humidity for the duration of the experiment. Whereas 50% of the males were down after 10 hours, 50% of the females were down only after 17 hours. Although all males were down in 18 hours, not all females were down in 30 hours. The peak of female activity occurred after 18 hours.

Exp. No. 2: One hundred-fifty ♀♀ and 70 ♂♂, 3-6 days old, were placed in separate desiccators at 23-25° C over calcium chloride. The initial R.H. of 25% dropped to 17% in one hour, 3% in 5 hours, 2% in 7 hours, and 0% after 18 hours. Whereas 50% of the males were down after 9 hours and 100% after 18 hours, 50% of the females were down after 18 hours, and 100% after 30 hours. The males reached their peak of activity (50% active) in 2-4 hours, while the females reached theirs (85% active) after 9 hours.

Exp. No. 3: One hundred-twenty ♀♀ and eighty ♂♂, 4-7 days old, were placed in separate desiccators at 23-26° C over calcium chloride crystals. Since the desiccators had been sealed for 8-12 days prior to use, the R. H. was down to 0% within 22 minutes after insertion of the mosquitoes. In this very dry air, 50% of males were down in 5 hours, and 50% of females in 22 hours. All of the males were down in 18 hours, whereas 50 hours were required for the females.

Exp. No. 4: This was the control experiment, carried out at 73% R. H. over 50% glycerin solution, using 115 ♀♀ and 50 ♂♂, 6-9 days old, in separate desiccators at 23-26° C. Although the other experiments used mosquitoes 4-7 or 2-6 days old, our experience has been that no appreciable difference in behavior exists within this age range of 2-9 days. At this favorable humidity, 50% of the males were down in 18 hours, and 100% in 33 hours, whereas for the females, 50% were down after 65 hours, and not all were down after 7 days.

TEMPERATURE

Experiments involving slowly rising temperatures.—In order to observe the reactions of adult *Anopheles* mosquitoes to gradually rising temperatures, separate groups of 90 ♀♀ and of 90 ♂♂ were introduced into the experimental chamber under controlled conditions of light and humidity. A relative humidity of 70-80% was maintained inside the chamber throughout the range of temperatures used. A gradient of 0-3° C

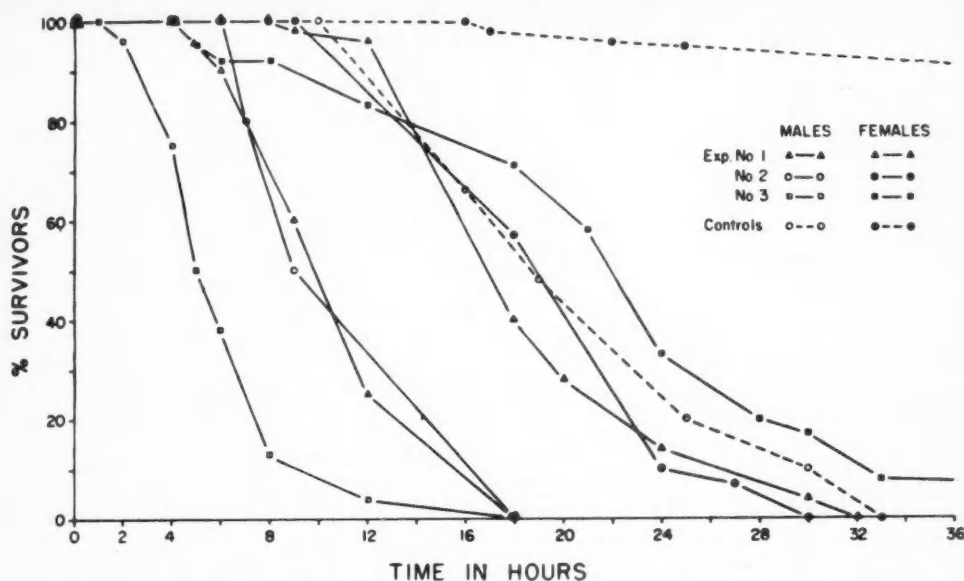


FIG. 4. Survival of mosquitoes in long-term exposures to dry air at room temperatures. Exp. No. 1 was conducted at 20-27% R.H.; Exp. No. 2 at 0-25% R.H.; and Exp. No. 3 at 0% R.H. Dotted lines represent controls, which were conducted at 73% R.H.

along the mid-section and 0-2° across the top of the experimental chamber exists when the entire length is used and water is contained in the humidity boxes at either end. Vertical temperature gradients non-existent at low temperatures but ranging up to 6° at high temperatures may exist from the bottom to the top of the tube. At relatively high temperatures these gradients are probably responsible for both the horizontal and vertical distributional patterns observed. All temperature measurements subsequently referred to are those with which the mosquitoes were in actual contact, i.e., the micro-temperature existing at the particular part of the tube where the observations were made. The air inside the chamber was cooled to 15° C and the mosquitoes introduced, after which the temperature was steadily raised to 50° C over a period of four hours.

As the temperature was raised the reactions of the mosquitoes were closely observed and recorded as to general behavior, degree of activity, and distribution in the chamber, horizontally and vertically. Population behavior patterns for short interval temperature rises were determined by analysis with reference to the following factors, each having five degrees of intensity: (1) per cent population in spontaneous flight (activity index); (2) response to mechanical stimulus (excitability); (3) flight characteristics; and (4) resting positions. The data are summarized in Figs. 5 and 6 and analyzed below. This analysis is especially desirable, since comparable information, to our knowledge, has not been published.

At temperatures up to 30° C the mosquitoes showed normal distribution, i.e., approximately one-fourth

1. ACTIVITY INDEX- (% pop. in spontaneous flight)	0-10%	11-20%	21-40%	41-60%	61-80%
	sluggish	slow	moderate	rapid	very rapid
	reluctant	occasional	restless	constant	erratic
	quiet upright	active upright	bouncing upright	sprawling	supine

FIG. 5. A device for analyzing population behavior patterns in gradually rising temperatures. Four factors are considered, each with five degrees of intensity. (Although the term "reluctant" under Flight implies will, a more apt one for this category could not be found.)

in the respective end sections and one-half in the middle five sections. Both males and females were very sluggish at the lower temperatures from 15 to 20°, exhibiting a slow response to a mechanical stimulus. There was little or no spontaneous flight activity and the mosquitoes assumed a quiet upright resting position. They tended to be vertically distributed on the top and sides of the tube, with the majority resting on the end walls. None was found resting on the screens over the humidity boxes at temperatures below 30° C.

The activity index increased with temperature rise, being very marked for both males and females between 20 and 30° C. Below 20° C there was very little movement of legs or mouth parts, whereas at 27-28° C there was some activity constantly, with most mosquitoes moving their legs while resting.

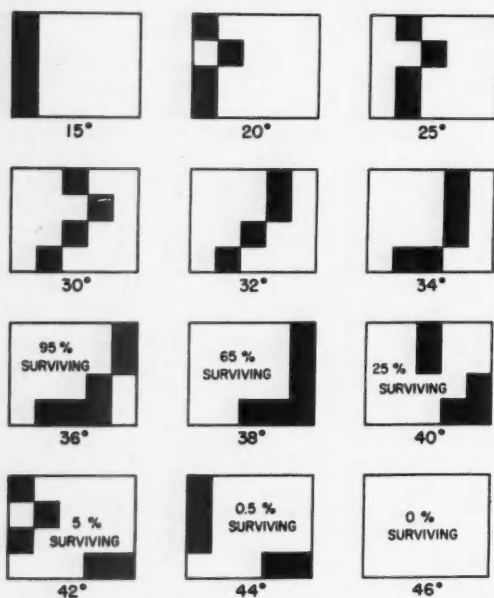


FIG. 6. An application of the analyzing device given in Fig. 5 for intervals of temperature rise from 15° to 46° C. The blacked-out squares for each interval correspond to equivalent values in Fig. 5. This analysis, refers only to the majority of mosquitoes surviving at a given temperature, and represents an average of male and female reactions to micro-temperatures as measured at specific positions occupied.

The range from 20-30° C roughly includes the temperature conditions which these mosquitoes experience in their natural habitat, and thus all reactions within this range can be considered more or less normal. Reactions above 30° C are markedly different, however, and require closer analysis with reference to interpretation of subsequent experimental results.

Above 30° C the mosquitoes became more restless, the activity index increasing from about 25% to a peak of about 75%, occurring for males between 35° and 38° C, and for females between 37° and 40° C. Beyond these peaks, activity became sporadic as the upper lethal temperature ranges were reached.

The pattern of response to a mechanical stimulus changed from sluggish below 20° C to moderate to rapid at 30° C and remained very rapid up to 38° C. Response then became progressively slower to 40-41° C, the surviving mosquitoes being very hard to disturb at these higher temperatures.

The manner of flight changed markedly above 30° C also. Around 30° C flight was unhurried with a searching movement, becoming almost constant from 34-36° C. Above 36° C the flight was agitated and rapid from one end of the tube to the other, mosquitoes bumping on the ends and perhaps pausing to rest a few seconds before flying again. From 38-40° C flight became erratic, mosquitoes going through

the middle of the tube in wide aimless swoops, then falling gently. At temperatures above 40° C flight was reluctant and when ventured was completely aimless.

An unusual hopping movement was exhibited by the mosquitoes as the temperature was increased, being first observed for males when the micro-temperature was between 33-35° C and for females between 35-37° C. This consisted of a continuous bouncing flight movement on the bottom of the tube and also on the wire screens. The great majority were found resting on the screens at micro-temperatures of 36-38° C, and mosquitoes tended to assume sprawled resting positions at this temperature, as if their legs were weakened. There was also much crawling. When the mosquitoes succumbed to the heat they generally assumed a supine position; usually regaining their feet once or twice, some to fly again before permanent knockdown.

Male mosquitoes were less resistant to the heat than females, approximately ¼ of them having fallen at 36° C and all at 40° C. About ½ of the females had succumbed in temperatures from 38-39° C, most of those surviving being sprawled on the screen. At this temperature and higher, mosquitoes were knocked down if they ventured away from the ends and attempted to fly through the hotter middle section of the tube. This fact notwithstanding, every mosquito seemed to be forced to leave the cooler positions and attempt flight, because no mosquitoes succumbed to the heat while resting on the screens. Most of the females were down at 42-43° C in the positions occupied, and one female survived to 44.5° C, resting at the left end of the tube.

There was a noticeable difference in the way mosquitoes were knocked down in flight as the temperature was raised. At the lower temperatures they seemed to hesitate in mid-air and spiral toward the bottom of the tube, hitting at an acute angle. At the higher temperatures they plunged to the bottom, hitting at almost right angles. It is interesting that the time and manner of knockdown correspond very closely to the results obtained subsequently in the experiments at constant temperatures. Heat undoubtedly increases the amount of energy expended in flight and in hopping movements and this in turn is closely correlated with the time of knockdown.

One very important observation obtained from this study on rising temperatures is concerned with the seeming ability of the mosquitoes to distinguish small differences in temperature. This was seen primarily in the tendency of the mosquitoes to choose the cooler sections of the tube as the temperature was raised above 30° C. Even at 30° C, when the temperature gradient across the tube was nowhere more than 2° C, the mosquitoes clustered at the cooler left end in flight and more were resting there. This observation was substantiated by reversing the inflow and outflow of water around the tube, making the right end 2° C cooler. A corresponding reverse in mosquito distribution was observed and also when

the flow was changed back to the original arrangement.

Experiments involving short-term exposures to a series of constant temperatures, at high and low humidities.—This group of experiments was organized as follows: 6-9 day old adult male and female mosquitoes, in samples of 30 individuals, were subjected to a series of high constant temperatures ranging from 35 to 49° C in atmospheres of high (70-73% R.H.) and low (20-30% R.H.) humidities. In order to reduce the temperature gradients inside the experimental chamber to a minimum for this series of experiments, several basic modifications were made. The two sections on either end were blocked off by placing two close-fitting cardboard partitions inside the tube 30 cm from each end, thereby utilizing only the middle five sections for the experiments. This procedure also made possible a more accurate control of humidity conditions inside the chamber by reducing the area involved.

Constant temperatures were maintained within the chamber by circulating water through the jacket surrounding the tube. Temperature gradients were determined inside the chamber along the bottom, midway, and top as the temperature of the water bath was raised from 30-50° C. A range of 0-1.5° C was found to exist along the bottom, 0-1° midway and 0-4° across the top of the tube. A vertical gradient, ranging from 0-3°, was found from the top to the bottom of the tube at any given position.

Relatively low humidities were maintained by placing a 15 mm layer of anhydrous calcium chloride crystals, which had been previously dried in a 100° C oven for one hour, in the bottom of the tube from end to end. This procedure at room temperature brought the R.H. down from 45% to 27% within one hour, and to 21% after six hours, where it was maintained for the next 72 hours. In all experiments involving low humidities there was a period of at least an hour between the time of placing the calcium chloride inside the chamber and the time at which the mosquitoes were inserted for observation. For maintaining relatively high humidities a 50% glycerol-50% water solution was used (Johnson 1940). A 9 x 66 cm strip of absorbent cotton was saturated with this solution, enclosed in a screen envelope to prevent mosquitoes from becoming stuck on the cotton, and placed across the bottom of the tube. The R.H. of the air inside the chamber was raised to 73% at room temperature within 30 minutes and fluctuated to within only 3.5% of this value when the temperature was raised to 55° C, falling to 69.5% at 47-50° C. It was not feasible to employ glycerol-water solutions which would produce humidities higher than 73% R.H. because the air inside the chamber became saturated with water vapor which condensed on the sides, causing mosquitoes to become stuck. Also, 73% R.H. more closely approximates natural humidity conditions encountered by adult mosquitoes. As with the low humidities, at least an hour intervened be-

tween the placing of the glycerol solution inside the chamber and insertion of the mosquitoes.

Mosquitoes were introduced into the chamber in lots of 5-10 individuals each for this series of experiments rather than in lots of 30, due to the difficulty encountered in making individual observations within the larger sample. Sufficient replicates were run to give a total of 30 mosquitoes for each separate experiment under a particular set of environmental conditions. Thus the number of individual observations totalled approximately 1700. Transfer of mosquitoes was carried out by means of a single tube aspirator and they were not etherized. When working with low humidities, calcium chloride crystals were placed into the aspirator in order to minimize the amount of moisture introduced when inserting the mosquitoes. Appropriate experiments indicated that insertion of mosquitoes in this way did not affect the R.H. beyond the normal limits of experimental variation as stated.

In analyzing the reaction of the mosquitoes to constant temperatures the behavior and degree of activity was recorded as before, but particular attention was paid to lethal effects of these high temperatures. An arbitrary exposure time of 20 minutes was chosen and the survival times of individual mosquitoes were checked by means of a stop watch from the moment of insertion of a sample into the chamber. These individual times were collectively expressed in terms of the percentage of the population surviving. The range of constant temperatures used for males and females at both high and low humidities extended from that temperature at which the whole population was knocked down within six seconds of the time of insertion to that temperature at which the whole population survived after 20 minutes. This is subsequently referred to as the upper lethal temperature range for mosquitoes, within these time limits. For 6-9 day old male mosquitoes at relatively low humidities (20-30% R.H.) this range was 36-47° C and for 6-9 day old females, 39-49° C. At relatively high humidities (70-73% R.H.) a range of 38-46° C was found for males and one of 39-47° C for females.

These data are plotted on four separate three-dimensional graphs (Fig. 7), using survival time in minutes as the abscissae and percent survivors as the ordinates, with temperature in degrees centigrade as the third-dimensional factor. The graphs thus depict the survival rates of male and female mosquitoes in the upper lethal temperature zone, at relatively high and low humidities. A detailed analysis of the data and comparison of reaction by temperatures is included here. Indicated temperatures represent those taken midway of the tube, vertically and horizontally.

The most marked variation in survival rates found in this series of experiments was that between males and females, at both high and low humidities. The female populations showed 100% survival for a 20 minute period up to 40° C, at which temperature the survival rate showed a gradual drop, decreasing to

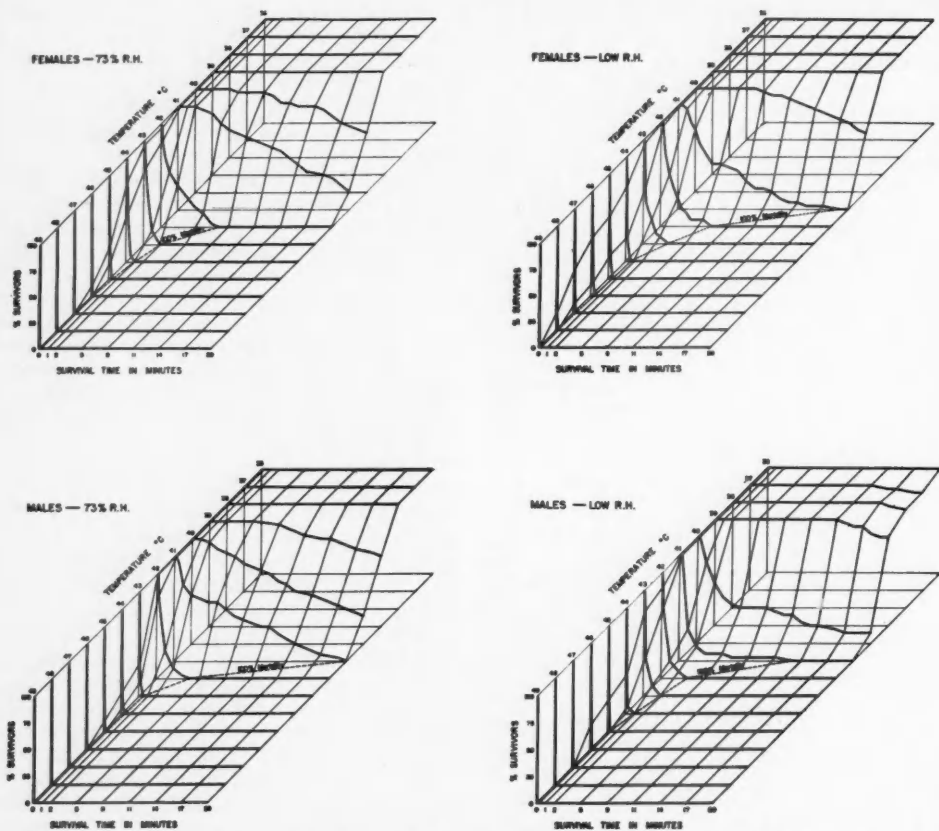


FIG. 7. Three-dimensional representations of survival rates in the upper lethal temperature zone for male and female mosquitoes at high and low humidities. The 100% survival lines for the non-lethal temperatures form a plateau to the rear in the upper right part of each diagram. The intermediate survival lines form a steep slope ending in a plain in the lower left part, beginning with the dotted 100% mortality curve.

57% after 20 minutes. At 41° C females showed 0-17% survival after 20 minutes. Above 41° C the decrease in survival rate at both high and low humidities was very sharp, 100% mortality being reached within 6-7 minutes at 42° C, 3-4 minutes at 43° C, and less than a minute at higher temperatures.

Survival rates for the male populations were markedly lower. The males showed 100% survival for 20 minutes at 36° C, 93-100% survival at 37 and 38° C, 67-83% at 39° C, and 10-27% at 40° C. Above 40° C for males, the decrease in survival rate was marked, 100% mortality being reached within 13-20 minutes at 41° C, 3-4 minutes at 42° C, ½-2 minutes at 43° C, and less than 30 seconds at higher temperatures.

In Fig. 8 the above results are shown in terms of 50% survival rates. The 50% survival time at 41° C for females at high humidity is 13 minutes, and for low humidity 4 minutes; for males at high humidity 6 minutes, and for low humidity only 1 minute.

Experiments relating to the influence of age, feed-

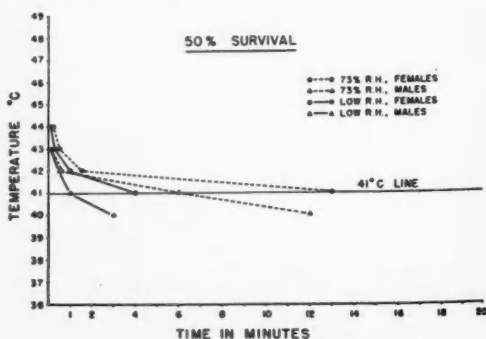


FIG. 8. Fifty per cent survival times at lethal temperatures. The lines are not continued to the right, since the next point for each would be off the graph. The 41° C line has been inserted for reference only. Note in text that at ambient temperatures the results are comparable, except that the 50% survival times are in hours rather than minutes.

ing, and sex on the lethal effects of high temperatures. —In order to determine the influence of age and feeding on the lethal effects of high temperatures, young male and female mosquitoes (2-3 days old) were subjected to constant temperatures of 40 and 41° C at 73% R.H., these having been determined to be critical temperatures at which a pronounced lethal effect began to be evidenced. Survival times were noted for a period of 20 minutes as previously described. The same procedure was followed for old (13-14 day-old) females and 7 day-old females which had been given blood meals 24 hours before.

Results of all experiments are summarized in Fig. 9. Analysis of these results and their comparison with data on 6-9 day old mosquitoes at 40-41° (as presented in Fig. 7) indicates small but fairly well marked differences in reaction to temperature among the various groups. No population showed 100% survival for 20 minutes, and all had some survivors after that period of time. The most noticeable variation was found in 6-9 day old males, which showed a considerably lower survival rate.

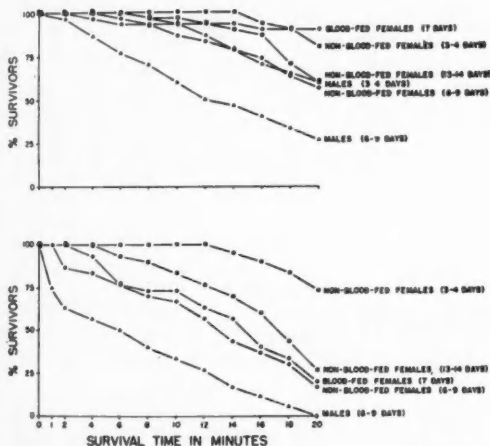


Fig. 9. Effects of age, feeding, and sex on survival rates at 40° C (upper figure) and 41° C (lower figure) in humid atmospheres (73% R.H.).

A comparison of the reaction of young and old mosquitoes, as seen in Fig. 9, indicates that young mosquitoes showed a 20-30% higher survival rate, mortality beginning 11 minutes later in females and 6 minutes later in males, at 40° C. At 41° C the young females showed a 55% higher survival rate and mortality began 10 minutes later.

The effect of a blood meal on the reaction of mosquitoes is seen by comparing results obtained using blood-fed females with that using both young and old females at 40 and 41° C. At 40° C the blood-fed females showed 90% survival after 20 minutes; 30% higher than the old females at 20 minutes and 13% higher than the young females. At 41° C the blood-fed and the old females showed about the same survival rate (20% after 20 minutes). The blood-fed

ones showed a 50% lower survival rate than the young ones at 20 minutes, however, with mortality beginning 10 minutes earlier.

Experiments pertaining to recovery from heat injury.—These experiments were designed to determine the relationship between the degree of heat injury and length of exposure to a lethal temperature. Assuming that the extent of injury would be expressed in terms of the amount of time required for recovery after removal to a favorable environment, mosquitoes were exposed to a temperature sufficiently high to produce immediate knockdown (in this case 45° C) and then removed for observation at specific time intervals by means of an aspirator from the experimental chamber to a desiccator maintained at room temperature. A relative humidity of 73% was maintained in both the experimental chamber and the desiccator by means of a 50% glycerol-50% water solution placed in the bottom.

Preliminary experiments carried out with individual mosquitoes indicated that females removed one minute from time of insertion revived to fly after one minute in the desiccator; those removed after three minutes revived after three hours but were very weak; while those removed after five minutes did not recover. Males removed 30 seconds to one minute from time of insertion recovered within 20-25 minutes; ones removed after two minutes were on their feet after 1½ hours but never gained strength to fly; those removed after three minutes responded to a stimulus after one hour but never recovered; and those removed after five minutes did not respond to a stimulus and were presumed dead. As a general rule, removal of mosquitoes while they showed any activity resulted in eventual recovery, but some mosquitoes, removed when all activity had stopped, revived after a sufficient period of time. These, however were usually in a weakened condition.

Using these as a basis, three sets of experiments dealing with population recovery from heat injury at 45° C were then run under the same environmental conditions, using 60 mosquitoes for each experiment. Thirty mosquitoes were removed between one and two minutes from the time of insertion, at the point when they were just knocked down but still active (referred to as Group I), and the other thirty were removed between four and five minutes from time of insertion, when all activity had ceased (Group II). These two groups of 30 each were placed in separate desiccators and observed for a 3 to 6 hour period to determine what percentage of the population recovered and the length of time required.

Results, as presented in Fig. 10, indicate that the mean percentage recovery for females in Group I after 30 minutes was 28%, 52% after 1 hour, 80% after 2 hours, 81% after 3 hours, 81% after 4 hours, 83% after 5 hours, and 83% after 6 hours. For males, 22% recovered after 30 minutes, 26% after 1 hour, 50% after 2 hours, 53% after 3 hours, and 53% after 4, 5, and 6 hours. There was no recovery for either sex in Group II after a period of 6 hours.

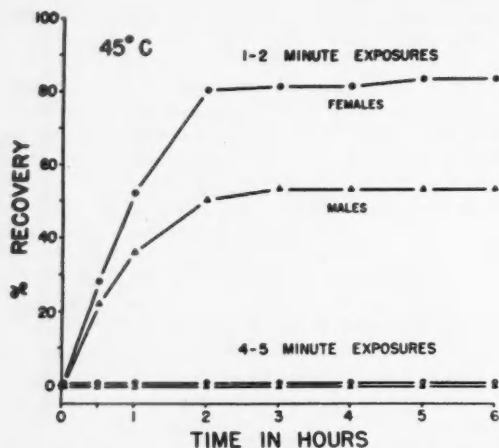


FIG. 10. Relationship between duration of exposure to 45° C and per cent recovery in hours after removal to favorable temperature and humidity.

LIGHT

Experiments involving varying intensities of white light.—Five lots of 30 adult female mosquitoes each of varying ages and physiological states were tested at light intensities varying between 0.3 and 500 foot candles, gradients being produced by placing incandescent lamps of various intensities at the ends of the chamber. No differential response was observed under these circumstances.

Since these experiments would indicate a reaction threshold to light intensity above 500 foot candles, one end of the tube was exposed to bright natural daylight at approximately 1500 foot candles, with the other portion covered with a dark cloth providing approximately 2-3 foot candles intensity. Under these circumstances the mosquitoes exhibited a marked negative phototactic response, more than 95% moving to the darkened end.

Many additional experiments were carried out on reaction to light intensity as an integral part of the studies described next on wave length. In one experiment an intensity of 0.025 foot candles, equivalent to moonlight, was placed in apposition to darkness and at another time to a higher intensity of 3.3 foot candles. No strong differential response at either end was noted, although a disproportionate number of mosquitoes moved to the ends of the tube. Subsequent experiments, such as those summarized in Part A of Table 3, also failed to demonstrate differential responses with respect to a wide range of intensities under 500 foot candles.

Experiments involving all colors at low intensities, using colored lamps.—The first series of experiments was designed to see if any preference could be elicited for any color when placed in apposition to other colors, using colored lamps at low intensities. Commercially obtained G.E. 3½ watt lamps, in triplicate, produced light intensities of 2-3 foot candles using

white, red, orange, yellow, green, and blue colors. Intensities were not further equalized.

Twelve lots were used, each consisting of 30 adult female mosquitoes 6-8 days old. Each lot was exposed to a series of experiments in which each color was placed in apposition to every other color—orange, for example, being placed in apposition to red, then to yellow, blue, green, and white. Thus a total of 5,400 observations were made on 360 individuals. Since the data, summarized in Fig. 11 have been treated statistically, detailed figures are not given for individual observations.

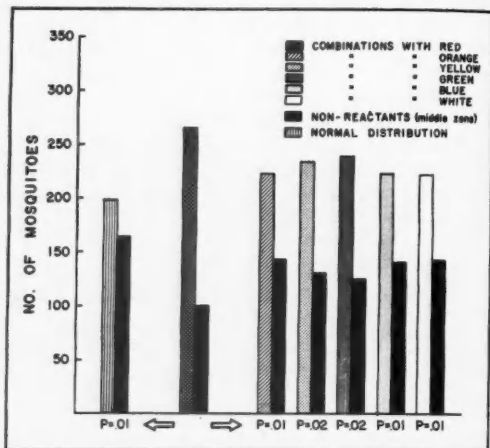


FIG. 11. Summary of distribution of mosquitoes within the chamber in response to various combinations of colors. In each case, the left-hand bar represents the total number of mosquitoes for the two end zones, whereas the right-hand bar represents those in the middle zone. Probability values are given for comparisons with red when used alone and in apposition to each of the other colors.

After extensive study of the data, two results seem clear. The first of these is that no statistically significant preference was shown for any color, each probability value being over the 50% level. That is, no preference was shown, for example, for red in apposition to blue, or for green when placed in apposition to yellow.

The second result concerns the distribution of mosquitoes within the chamber. In experiments involving all colors with the exclusion of red, the distribution of mosquitoes within the chamber was not significantly different from the normal distribution, the probability values being above the 10% level. However, when red was used alone or in apposition to any other color, there was a statistically significant difference ($p = 0.01$) from the normal distribution—72.2% of the mosquitoes being in the ends as contrasted to the normal distribution of 54.5% of mosquitoes in the ends. Comparison between responses to all colors in apposition to red and all in apposition to orange yielded a probability value

TABLE 3. Experiments involving red, blue, and darkness in apposition to each other.

A. High and unequal light intensities using Bourges Filters.

Blue vs. Red at 120-250 foot candles

Number individuals	Number replicates	Total number observations	Age (days)	DISTRIBUTION		
				Blue zone	Middle zone	Red zone
30	3	90	3	30% blue, 225 f.c.		100% red, 120 f.c.
30	3	90	4	27	35	28
				22	25	43
30	3	90	3	30% blue, 225 f.c.		30% red, 250 f.c.
				22	41	27
30	3	90	4	50% blue, 215 f.c.		30% red, 250 f.c.
30	3	90	4	41	28	21
30	3	90	4	30	42	18
30	3	90	4	50% blue, 215 f.c.		100% red, 120 f.c.
				23	35	32
180	18	540		165 (31%)	206 (38%)	169 (31%)

B. Low and equal light intensities, using Bourges Filters.

Blue (50%) vs. Red (100%) at 1.4 foot candles

				Blue zone	Middle zone	Red zone
30	3	90	4	24	24	42
30	3	90	4	25	39	26
30	3	90	3	33	22	35
30	3	90	4	41	19	30
30	3	90	4	31	24	35
30	3	90	3	26	17	47
180	18	540		215 (40%)	145 (27%)	180 (33%)

Blue (50%) vs. Darkness at 1.4 foot candles

				Blue zone	Middle zone	Dark zone
30	3	90	4	34	32	24
30	3	90	3	41	23	26
30	3	90	4	36	27	27
30	3	90	3	37	26	25
30	3	90	4	52	9	29
30	3	90	5	40	29	21
180	18	540		240 (45%)	146 (27%)	152 (28%)

Red (100%) vs. Darkness at 1.4 foot candles

				Dark zone	Middle zone	Red zone
30	3	90	4	29	34	27
30	3	90	3	26	29	35
30	3	90	4	31	32	27
30	3	90	4	43	16	30
30	3	90	4	38	16	36
30	3	90	3	28	21	40
180	18	540		195 (36%)	148 (28%)	195 (36%)

C. Low and equal light intensities, using monochromatic filters.

Blue vs. Red at 0.5 foot candles

				Blue zone	Middle zone	Red zone
30	3	90	6 - 10	38	17	35
60	3	180	8	85	36	59
60	3	180	5 - 6	61	42	77
30	3	90	6 - 10	46	27	17
30	3	90	6 - 10	42	19	29
60	3	180	6 - 10	66	70	44
270	18	810		338 (42%)	211 (26%)	261 (32%)

Blue vs. Darkness at 0.5 foot candles

				Blue zone	Middle zone	Dark zone
30	3	90	6 - 10	49	20	21
60	3	180	8	91	37	52
60	3	180	4 - 8	92	61	37
30	3	90	6 - 10	38	25	27
30	3	90	6 - 10	36	27	27
60	3	180	6 - 10	80	58	42
270	18	810		386 (47%)	228 (28%)	206 (25%)

Red vs. Darkness at 0.5 foot candles						
Number individuals	Number replicates	Total number observations	Age (days)	DISTRIBUTION		
				Dark zone	Middle zone	Red zone
30	3	90	6 - 10	28	19	43
60	3	180	8	62	33	85
60	3	180	5 - 6	68	39	73
30	3	90	6 - 10	27	40	23
30	3	90	6 - 10	39	27	24
60	3	180	6 - 10	39	63	76
270	18	810		263 (33%)	221 (27%)	324 (40%)
Red vs. Darkness at 4.0 foot candles						
Number individuals	Number replicates	Total number observations	Age (days)	DISTRIBUTION		
				Dark zone	Middle zone	Red zone
60	3	180	5 - 6	76	45	59
30	3	90	6 - 10	36	31	23
30	3	90	6 - 10	43	24	23
60	3	180	6 - 10	76	56	48
60	3	180	4 - 8	75	51	54
30	3	90	4 - 8	41	26	23
270	18	810		347 (43%)	233 (29%)	230 (28%)

of $P = 0.01$; yellow, $P = 0.02$; green, $P = 0.02$; blue, $P = 0.01$; and white, $P = 0.01$ (Fig. 11). This increase could be attributed either to the fact that more mosquitoes are attracted to the light, or that the presence of red has a stimulating effect upon flight, with the result that mosquitoes in undirected flight tend to congregate at the end walls.

Experiments involving red, blue, and dark at unequal intensities, using Bourges filters.—Another series of experiments was carried out utilizing incandescent light filtered through various Bourges standardized colotone sheets in 100% and 30% poster red and 50% and 30% process blue. One of the principal reasons for using these filters is that their large size of 18 x 24 inches makes it possible to place behind them high-wattage incandescent lamps, thus permitting much higher light intensities than was possible with low-wattage colored lamps. Although these filter sheets are not monochromatic, they do have a high transmission peak in their respective colors. The per cent of color is that percentage impregnated in the sheets, which in turn alters the intensity of the light transmitted. The sheets were arranged on wooden frames projecting over the light bulbs at either end of the black box.

In the first experiments, light intensity inside the tube, produced from single 7½ watt white bulbs at either end, varied from 1.4 to 3.4 foot candles, depending upon the filter used. The various intensities of blue and red were placed in apposition to each other and to dark.

A second series of experiments was carried out utilizing three 100 watt bulbs at either end, which produced intensities from 120 to 300 foot candles, again depending upon the particular filter used. Each color was similarly tested against other colors and against darkness, again without intensities being equalized.

In all of these, no consistent preference was noted

for any particular color. The data are summarized in part A of Table 3.

Experiments involving red, blue, and dark at low equalized intensities, using both Bourges filters and monochromatic filters.—The above experiments were designed to demonstrate strong color preferences only, and therefore could not determine slight population preferences, if present, for monochromatic light at equalized intensities. Accordingly, three series of experiments were set up in which only red, blue, and dark were used. Light intensities at either end were carefully equalized for each series, at 0.5, 1.4, and 4.5 foot candles. Spectral transmission curves were made for the 100% red and 50% blue Bourges filters, and for the red and blue monochromatic filters, using a Model DU Beckman Spectrophotometer (Fig. 12). All data are tabulated in parts B and C of Table 3 and are graphically summarized in Fig. 13. A total of 42 separate experiments involving 5,860 observations on 690 individuals were carried out.

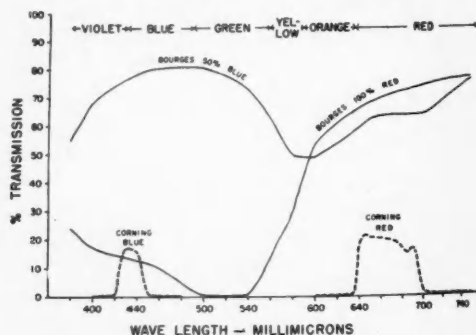


FIG. 12. Visual transmission curves for 50% blue and 100% red Bourges filters and Corning narrow band pass blue and red filters as determined by a Model DU Beckman Spectrophotometer.

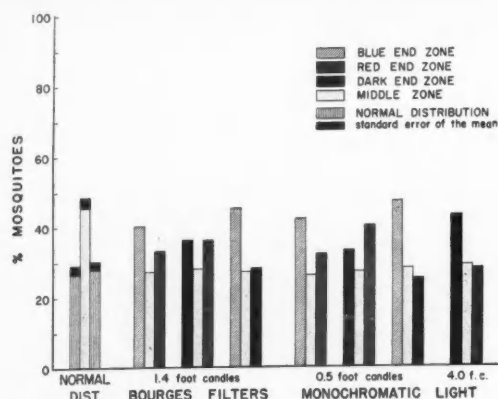


FIG. 13. Reaction of mosquitoes to red, blue, and dark at equalized intensities, using Bourges filters and monochromatic light. Results are compared with the normal distribution.

The data on these experiments may be summarized as follows: (1) in all experiments contrasting blue with red at equalized intensities ranging from 0.5 to 1.5 foot candles, a preference is shown for blue; (2) in comparable experiments contrasting blue with dark, a strong preference is exhibited for blue; (3) on the same basis, however, little distinction is made between red and dark, a preference being demonstrated for red at 0.5 f.c., for dark at 4 f.c., and for neither at 1.4 f.c.; (4) thus the order of preference places blue first, then red, then dark; (5) the series of experiments with monochromatic light did not differ greatly from the series using Bourges filters, though results for specific colors were sometimes reversed; (6) the number of mosquitoes occurring in the ends were usually much higher than that obtained for the normal distribution.

Experiments involving color temperatures from 0-26,500° K.—By the use of appropriate combinations of overhead fluorescent lamps, natural light conditions were set up in the chamber, ranging from before sunrise through the day to sunset. Thus, different color temperatures were not set in opposition to each other, but rather other factors were varied for each sky condition used.

Within the whole range of relative humidity gradients, in each of which color temperatures of 0-26,500° K were produced, the mosquitoes showed no significantly different responses from those tested in the same relative humidity gradients without the use of color temperatures. All probability values here were above the 70% level. At constant humidities of 45%, 60%, 72%, 85%, and 95% the mosquitoes exhibited no significantly different responses from those obtained at these constant humidities without the use of color temperature. All probability values here were above the 80% level. All of these results were temperature independent over the range of 15-32° C. Likewise, no differences were noted between various

color temperatures used under constant conditions of temperature and light.

Since these studies involved 216 separate experiments, the negative results obtained under the conditions stated are well substantiated.

Experiments involving the effects of temperature and humidity upon phototactic response.—All three characteristics of light—intensity, wave length, and color temperature—have been checked throughout their ranges against the full range of humidity, and against ambient temperatures from 15 to 32° C. In every case light behavior was unaltered by any combination of temperature and humidity used.

DISCUSSION

GENETICAL AND ECOLOGICAL CONSIDERATIONS

Although laboratory aspects of ecological studies are legitimately derived from a number of objectives, their ultimate objective should be expressed in terms of the natural behavior of the organism under consideration. Thus, this section constitutes a critical analysis of the use of data obtained on these laboratory populations to the understanding of natural populations.

Very few experimental studies have been carried out on population genetics of mosquitoes. However, studies on other insects and on various animals and plants have provided certain valid generalizations. Dobzhansky (1951) and Andrewartha & Birch (1954) have given excellent reviews of population genetics, with particular reference to insect populations.

The principle is well established that relative frequencies of different genes may differ significantly between populations of the same species which occur in different places or in the same place but at different times. For example, the populations of *A. quadrimaculatus* first emerging in the spring in the mild climate of the southern states come from over-wintering adults. Since a fairly rigorous selection has been going on over winter in the survival of these few, it is quite probable that the gene frequencies in their offspring would be different from those produced in late summer where a different set of selective mechanisms have been operating through the hot period of the year. Likewise, of course, *A. quadrimaculatus* populations in southern Canada would in all probability have different gene frequencies than those in the semi-tropical areas of this country. Such geographic and seasonal changes in relative gene frequencies for other organisms have been correlated independently with many environmental factors. These include, according to the above-cited reviews, temperature, moisture, and light; interactions with other geographic races; food; numbers of other individuals of the same species; numbers of other individuals of different species; ecological niches; and other components of environment, including insecticides.

Thus, the primary objections, i.e., changes in gene frequencies, raised against the utilization of data gained on laboratory-bred populations could be

leveled equally well against data obtained for a given time or locality on wild-caught populations, with two exceptions. The first is that the genetic plasticity of the wild-caught species would probably be greater because of the much increased size of the inter-breeding population, and secondly, factors of selection are those normally operating in nature, whereas factors operating in domesticated strains include those imposed by man.

Two additional limitations to these laboratory studies are: first, that they show but a small part of the interaction between the entire environmental complex and the genetically controlled physiological characteristics of the experimental organism. They are not concerned with the effects of the factors studied on other stages in the life cycle, nor do they show the effects of population pressure in nature. Secondly, it has been impossible throughout this investigation to compare the results obtained on the laboratory strains with wild-caught populations, as was planned when this investigation was initiated. There has been an almost total, though probably temporary, decimation of the wild populations of *A. quadrimaculatus* in Georgia, because of three successive drought years (1953, '54, '55), the third being the worst recorded for this century. This likewise accounts for the fact that we have no publishable data for this species from the field laboratory which has been in operation during this time.

On the other hand, these laboratory studies have decided advantages. Investigators have generally agreed that temperature, moisture, and light are the primary factors operating in the life of the adult mosquito, yet an appraisal of the physiological tolerance of adult mosquitoes to these factors, singly or in various combinations, is difficult, if not impossible, to obtain in nature.

Laboratory studies on the orientation reactions of adult mosquitoes to environmental factors are relatively few in number, and none have been found which deal with more than two factors at one time. This study is unique in that either gradients of or constant conditions of temperature, humidity, and wave length, intensity, and color temperature of light have all been used simultaneously in many combinations. Also the entire population, rather than strongly reacting segments only, have been used in presenting the results.

Variability within the experimental samples has been surprisingly wide and is of definite ecological significance. In none of our experiments did the entire sample demonstrate a uni-directional, or even a directional response. Rather, individuals were present in all three parts of the chamber, the two ends and the middle. Such wide variability probably corresponds to their reaction under natural conditions. It would not be difficult to set up either-or choices in such a way that a very large segment or perhaps all of a given sample would react in the same way. For example, a choice of 1 versus 10,000 foot candles of light, or of 0 versus 75% relative humidity would

almost of certainty yield a total response. But such violent contrasts are seldom encountered in nature. Rather, the environment consists of various combinations and, through time, various series of combinations of intensity spans more nearly of a magnitude employed in this study.

LABORATORY FINDINGS

Response to relative humidity was pronounced, although considerable variability was demonstrated between individuals, and with single individuals, as a few of them moved up and down the gradient. Since many insects have demonstrated a response to vapor pressure, or absolute humidity rather than relative humidity, response to relative humidity by this species is of interest.

While running the experiments on relative humidity gradients, replicates were made so as to subject the mosquitoes to a wide range of colors, intensities, and color temperatures of light for each of the several humidity gradients set up, at temperatures ranging from 15 to 32° C. In no case was there any evidence of any of these parameters of light having any effect on humidity preference. Response to relative humidity was also independent of temperature at ambient or near-ambient temperatures from 15-32° C. This was determined by running the whole series of relative humidity gradients at approximately 5° C intervals within this range. Our finding agrees with Brown (1951) who found in field studies with *Aedes* mosquitoes that above 15° C moisture was the chief attractant factor.

At lethal or sub-lethal temperatures, above 35° C, where death occurs within a few seconds to an hour's time the opposite is true, temperature being the primary factor in mosquito response, individuals frequently demonstrating an ability to distinguish between as little as 1° C temperature gradients. However, moisture has a definite effect in relation to the time required for death at a given temperature. Examination of Fig. 8 clearly indicates this, where for example at 41° C, 50% of the females survived at high humidities for 13 minutes, but only for 4 minutes at low humidities.

The principal effect of atmospheric moisture for short periods of time at these high temperatures could result from moisture loss from the body. Results indicate that these mosquitoes probably lack a moisture-conserving mechanism, or at least lack a very efficient one. As evidenced by Lewis' (1933) experiments on *Aedes aegypti*, most mosquitoes belong to the class of insects which do not possess an efficient mechanism for retarding loss of water by evaporation over long periods of time. Lewis believes they do not require such a mechanism because their mode of life is such that they can readily take in water, either by drinking it or by sucking blood or plant fluids in both sexes.

Even at ambient temperatures, low humidities over long periods of time are detrimental, those near zero being about as detrimental as those at zero, un-

der the conditions stated. Also, females are much more resistant than males to low humidities, with males having a correspondingly shorter life span under favorable conditions of temperature and humidity.

The results obtained in the series of experiments in which mosquitoes were subjected to gradually rising temperatures, from ambient through lethal, make an interesting comparison with those obtained in the experiments using reactions to constant temperatures over the same range. The results basically support each other, since the same lethal temperatures operate for the majority of the populations in both cases. For instance, the survival rate of the male mosquitoes decreases rapidly from 37-38° C in the rising temperature experiments, whereas 39-40° C was found to be the critical temperature for males in the constant temperature series. The fact that mosquitoes were exposed to heat for a longer period of time in the rising temperature experiments is probably responsible for the differences in survival observed. This longer exposure could possibly have the effect of increasing the heat injury, or acclimatizing the mosquitoes to higher temperatures. When evaluating and comparing the results of these two sets of experiments, it should be kept in mind that the observations on survival do not fall within absolute limits, and that survival rates were calculated on the basis of 150 ♀♀ and 90 ♂♂ in the rising temperature experiments and on 54 groups of 30 individuals each in the constant temperature experiments.

Behavior observed at various constant temperatures corresponded very closely to that observed at rising temperatures. Both the rapidity and frequency of knockdown after insertion at constant temperatures were observed to increase as the temperature was raised. Males generally fell gently within 30 seconds after insertion at 40-41° C and revived to fly before permanent knockdown; females at 40-41° C fell initially within 1-15 minutes after insertion, some staying down for 7-8 minutes, but revived to fly again. From 42-45° C males fell sharply soon after insertion with only sporadic flights by a few individuals being observed afterwards. Above 45° C no sporadic flights after knockdown were observed. Females fell sharply from 44-46° C, with a small percentage reviving to fly sporadically; at 47° C and above they fell immediately and stayed down.

At lethal temperatures, it is interesting to note that not only moisture and sex, but also age and feeding have pronounced effects on survival times at particular temperatures.

Experiments pertaining to recovery from heat injury are quite interesting in that there is a fairly sharp cut-off point at which recovery may take place. For example, at 45° C mosquitoes when introduced are immediately knocked down and are apparently dead, but most will revive within a few hours, when the exposure is for 2 minutes, but will not survive at all if this exposure is increased to 5 minutes. If the lethal effects of high temperatures are due pri-

marily to denaturation of proteins, then the results of these time-temperature experiments may shed some light on the time relationship of the denaturation process.

The fact that *A. quadrimaculatus*, a night-flyer, is negatively phototropic has added interest to, as well as increased the technical difficulties encountered in, the series of experiments designed to determine the extent to which the species is reactive to radiant energy, especially at the low light intensities under which it is normally active. In reviewing this range of studies, the results have been interesting if somewhat baffling. There has been little or no consistent response to differences in intensity up to 500 foot candles, very little or no consistent response to wave length, except a slight one to blue, an excitation in the presence of red and blue, and no response at all to color temperature.

More attention has been given to determine their reactions to color than any other light factor. From the several series of experiments with color, four conclusions may be drawn. (1) Great diversity exists not only between separate samples, but between groups of samples with regard to the relative attractancy of various wave lengths. If we assume a chance distribution comparable to the normal distribution given in Fig. 13, then only a small per cent of the population in any case was positively motivated. (2) Data analysis strongly indicates that the reaction is always either positive or indifferent, never negative, i.e., repelling. (3) When the data are analyzed for attractancy to brightness, or to shorter versus longer wave lengths, the results coincide with those on colored lamps having wide spectral emission bands, thus making it impossible to distinguish between these three factors. Of interest, however, is the fact that in 24 experiments using 30 and 100% red and 30 and 50% blue Bourges filters, at unbalanced intensities ranging from 1.4 to 250 foot candles, there were no consistent preferences, a grand total of all 24 yielding an exact balance between red and blue. (4) The existence of blue or red light excites the mosquitoes to greater activity, though undirected, with the result that greater numbers consistently occur in the ends over that obtained for the normal distribution, or for the distribution usually observed in uniform white light.

Adequate checks would have to be made on wild species before the relative validity of these findings could be established. It may well be that this adequately represents reactions of wild populations, their actually having little response except to fairly sharp contrasts in intensity. On the other hand, there may be some genetical change, due to shifts in gene frequencies resulting from domestication of the wild strain. The whole subject, however, is worthy of much more attention, and we have hardly made a beginning here. Other groups of factors which may affect an insect's reaction to light have been enumerated by Weiss (1943) as follows: previous exposure to light, angle of incidence, variations in sen-

sitivity of different parts of the compound eye, position of the iris pigment and the rate of pigment migration in relation to light intensity, temperature, moisture, and air currents, chemotropism, its variable physiological state, the stimulation of sense organs other than the eyes, the influence of the central nervous system and the wave length and intensity of the radiation to which it is first exposed.

CORRELATION WITH NATURAL ENVIRONMENT

The available data will not permit detailed correlations of mosquito behavior through successive hours of the day and night at different elevations and in different habitats, i.e., microenvironments, but they will permit characterization of behavior in terms of extremes of environmental conditions.

Field observations indicate that this behavior can be evaluated in two respects; the first with regard to their daytime environment when the adults are resting in secluded places, and the second with regard to their nighttime environment, roughly from sunset to sunrise, when flight, feeding, mating, ovipositing, and other essential life activities are being carried out.

Resting behavior, daytime.—Extremes of high temperatures which often surpass the lethal point are attained only during the warmer periods of the year and then only during the day. Thus, wild populations of *A. quadrimaculatus* have only to contend with these during their resting time. In studies during July in western Tennessee, Eyles & Bishop (1943) found that the temperatures of natural resting areas were regularly 4 degrees centigrade or more cooler than the atmosphere immediately outside of such resting places. Our studies on temperature tolerance indicate a lethal range above 37° C. Maximum temperatures observed in resting habitats at 3 or more feet above the ground level have not exceeded 40° C, and usually range from 30 to 35° C. On the other hand, in open areas temperatures immediately above the surface of the ground may reach 60 or more degrees C, with temperatures several inches above the ground at 40-50° C. Therefore, on warmer summer days, the probability exists that adults cannot leave their resting places and still survive.

Although temperature is the only factor which apparently absolutely restricts distribution of adults to resting places during the extremes of daytime environment, our experiments also indicate the existence of strong preferences for those conditions of moisture and light obtaining in resting places as contrasted to that outside either in the woods or open field. Relative humidity, even in densely wooded and swampy areas, rarely exceeds 60% during the warmer hours of the day, and in open woods and fields is usually much lower. Our measurements, as well as those by Eyles and Bishop, indicate a difference of 8-10% or more relative humidity during the day between the resting places and adjacent outside areas.

The experimental populations demonstrated a strong avoidance reaction to bright light. Resting

places rarely exceed a few foot candles, whereas full sunlight intensity may exceed 10,000 foot candles.

Activity behavior, nighttime.—An interesting question is why do adults leave their resting places sometime before dark, and return to them early the following morning. Both parts of this question cannot be answered by the same set of data. Obviously, should they fail to return in the morning on a warm day, death or extreme discomfort may result. On the other hand, failure to leave in the late evening would have no such adverse effects. In thinking of the three primary factors of temperature, moisture, and light, light is the only one which undergoes marked change both after sunset and prior to sunrise continually throughout the breeding season. The more pronounced gradients of temperature and humidity associated with sunset and sunrise occur prior to the principal egress of mosquitoes in the evening and subsequent to their ingress in the morning. Eyles & Bishop (1943) found in field studies of wild populations of *A. quadrimaculatus* that the only microclimatic condition which could be correlated with their principal egress from resting places in the evening and their subsequent ingress in the morning was that of light intensity. At the time of most rapid exodus, light intensities in the open varied from a mean of about 48 foot candles at sunset to 2 foot candles 20 minutes later. They could make a large portion of the mosquitoes remain throughout the evening by artificially lighting the diurnal shelter. During the hours just after sunrise, they found that females tend to enter the resting places in a gradual rather than a concerted manner, the exact time apparently depending upon when direct sunlight struck the mosquitoes in the open.

In the evening and in the morning, light varies of course not only by its intensity but also by its color. Since there is a decided shift at evening to the longer wave lengths of the spectrum, one would expect the adults to show a marked preference for colors of longer wave lengths if this were a deciding factor in their morning and evening behavior. Our experiments on laboratory populations would indicate that such is not the case. Their response to color was very poor, for in no case did a large segment of the population demonstrate a preference for one color over any other color. In studies with monochromatic light, the experiments would indicate that the mosquitoes cannot distinguish between red and black. Their preference, if any, was toward intensity and brightness rather than color, which is in line with findings obtained for other species and other insects. Extensive experiments on color temperatures again failed to elicit a definitive response, when these were made to conform to natural sky colors ranging from several minutes before sunrise to cold blue north skies. It is interesting that red, although eliciting no directional response at all, did induce a state of excitability over that indicated by other colors. This may be therefore a contributory stimulus, though not a primary one, in the egress from resting places.

Laboratory experiments on temperature effects have indicated that maximum activity was reached at temperatures of 30 to 35° C. Such temperatures correspond to those usually obtaining throughout the warmer nights of the breeding season. Likewise their preferences for humidity of 70-80% more nearly coincides with humidities obtaining through the night in their natural habitats.

Since adults of this species frequently fly a mile or more from the breeding area to a feeding site, the question arises as to the micro-environment through which such flights take place. Although they often occur across open fields, they occur at night and thus conditions of temperature and humidity, though not necessarily at the optimum, certainly do not fall near the critical or lethal zone.

SUMMARY AND CONCLUSIONS

Laboratory studies have been conducted on the reaction of *Anopheles quadrimaculatus* Say to various combinations of moisture, temperature, and wave length, color temperature, and intensity of light.

The optimum relative humidity was found to be between 70 and 80%, there being a sharp avoidance of higher as well as of much lower humidities. In comparison with vapor pressure and absolute humidity, relative humidity proved to be the critical factor. These reactions were not influenced by variations in light intensity and color, and were temperature independent over the range of 15 to 30° C. At both ambient and lethal temperatures, relative humidity had a pronounced effect upon survival. At ambient temperatures, 50% survival time at high humidity was 65 hours for females and 18 hours for males, while at low humidity the 50% survival time was reduced to approximately 20 hours and 8 hours, respectively. At the much higher temperature of 41° C, the 50% survival time for females at favorable humidity was only 13 minutes and for low, 4 minutes; for males, 6 minutes and 1 minute, respectively.

Tolerances to high temperatures of 37-49° C, expressed as percentage population surviving in arbitrary exposure times of 20 minutes, ranged from 100% mortality within 6 seconds to 100% survival after 20 minutes. Lethal temperatures for most individuals was from 40-44° C, with consistent differences noted for sex and humidity. At these same temperatures, young mosquitoes were more resistant than older ones, and blood-fed females somewhat more resistant than non-blood-fed ones.

Population behavior patterns for short interval temperature rises were determined on the basis of percent population in spontaneous flight, response to mechanical stimulus, flight characteristics, and resting position. Male mosquitoes showed the greatest activity between the temperatures of 35 and 38° C and females between 37 and 40° C.

Females also have a better recovery rate than males from exposures to high temperatures. At 45° C approximately 80% females and 45% males recovered from a 1-2 minute exposure within a period of several

hours, but when increased to 4-5 minutes, there was no recovery in either sex.

With regard to light, individual variability was very high and little or no consistent population response was noted to differences in intensity up to 500 foot candles, nor to brightness, color temperature, or wave length, except a slight preference for blue and an undirected excitation in the presence of red and blue. The response was always positive or indifferent, never negative (repelling).

The behavior of natural populations is analyzed with reference to daytime (resting) and nighttime (activity) environments. Although temperature is the only factor which restricts adults to resting places during the day, strong preferences are also noted for the higher humidities and lower light intensities prevailing in these locations. Temperatures and humidities obtaining at night during warm periods of the year coincide very closely with optimum conditions as determined in the laboratory. Light intensity is the only micro-climatic condition which can be correlated with egress from and ingress to resting places.

The population variability occurring within the physiological limits established by this investigation is high in terms of mosquito behavior studies previously published and indicates the existence of broad ecological amplitudes with respect to the conditions studied.

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